National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

UNIVERSITY OF ALBERTA

REVISION OF THE PERCOPHID GENUS BEMBROPS (OSTEICHTHYES, PERCIFORMES): TAXONOMY, OSTEOLOGY, PHYLOGENY AND BIOGEOGRAPHY

BY

MRINAL K. DAS

©

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

CANADA

SPRING 1993

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-82240-6

Canada

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF THE AUTHOR:	MRINAL K. DAS
TITLE OF THE THESIS:	REVISION OF THE PERCOPHID GENUS BEMBROPS (OSTEICHTHYES, PERCIFORMES): TAXONOMY, OSTEOLOGY, PHYLOGENY AND BIOGEOGRAPHY
DEGREE:	DOCTOR OF PHILOSOPHY
YEAR THIS DEGREE GRANTED:	SPRING 1993

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as hereinbefore provided neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Mrinal K. Das

147 Beleghata Main Road

Calcutta 700 010

INDIA

24 March 1993

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **REVISION OF THE PERCOPHID GENUS BEMBROPS (OSTEICHTHYES, PERCIFORMES): TAXONOMY, OSTEOLOGY, PHYLOGENY AND BIOGEOGRAPHY** submitted by **MRINAL K. DAS** in partial fulfillment of the requirements for the degree of **DOCTOR OF PHILOSOPHY**.

Joseph S. Nelson

Dr. Joseph S. Nelson
Supervisor

Mark V. H. Wilson

Dr. Mark V. H. Wilson
Member, Supervisory Committee

John R. Spence

Dr. John R. Spence
Member, Supervisory Committee

Richard C. Fox

Dr. Richard C. Fox
Examiner

Jan O Murie

Dr. Jan O. Murie
Examination Chairman

for Jan O Murie

Dr. Tomio Iwamoto, External Examiner
California Academy of Sciences

24 March 1993

ABSTRACT

Bembrops, a percophid genus, is a monophyletic group of 13 species of marine teleosts found in the continental shelf and slope areas of tropical and warm temperate regions of the Indo-West Pacific and Atlantic between depths of approximately 50 and 700 m.

To study the morphological variation and validity of all 18 nominal species in the genus and the interrelationships of the valid species, principal components analysis was performed using 26 traditional morphometric, 21 truss, and 14 meristic characters, and two attributes. A number of meristic characters and attributes (including pigmentation on membranes between the spines of the first dorsal fin) were useful in identifying the species. Most of the morphometric and truss characters contributed very little in discriminating different species groups. Based on the results of the morphometric study and detailed examination of all nominal species, five nominal species, B. adenensis, B. aethalea, B. filodorsalia, B. indica, and B. philippinus, were synonymized with other species. The osteology of Bembrops anatirostris has been described in detail for the first time and compared to that of other species of Bembrops and four other percophid species.

A phylogenetic analysis was undertaken and cladograms were constructed using 54 morphological and osteological characters by making outgroup comparisons with four other percophid species - Percophis brasiliensis, Chrionema chlorotaenia, C. squamiceps and Hemerocoetes pauciradiatus. Bembrops, Chrionema and Hemerocoetes form a monophyletic group on the basis of seven synapomorphies. The sister-group relationship of Bembrops and Chrionema was supported by seven synapomorphies. The monophyly of all members of Bembrops was supported by four synapomorphies. Within the genus, three species groups are recognized.

The distributional patterns of 13 species are discussed from the points of view of three major biogeographic methodologies. Area cladograms derived from the phylogeny of the genus and generalized distribution tracks were analyzed. It was inferred that both dispersal and vicariance can explain the present-day distribution of the species of the genus.

ACKNOWLEDGMENTS

This dissertation would not have been completed without the guidance, supervision and inspiration of my supervisor, Dr. Joseph S. Nelson. I express my deepest gratitude to him for being an excellent mentor and for providing constant support, encouragement, and enthusiasm.

The members of my supervisory committee, Dr. Mark V. H. Wilson and Dr. John R. Spence, provided helpful comments and advice throughout the course of this study. I wish to extend my sincere appreciation and regards to them. I am grateful to my external examiner, Dr. Tomio Iwamoto, examiner, Dr. Richard C. Fox, and examination chairman, Dr. Jan O. Murie for useful suggestions and insights.

One cannot conduct a systematic study of a marine fish genus in "landlocked" Edmonton without the help and cooperation of numerous individuals and their institutions. I wish to thank all of them for the loan and/or donation of specimens pertinent to this project: Dr. Mark McGrouther, and Dr. John R. Paxton, Australian Museum (AMS); Dr. Alwyne Wheeler, and Dr. Peter J. P. Whitehead, British Museum (Natural History) (BMNH); Ms. Jane B. Culp, Dr. John E. Randall, and Dr. Arnold Y. Suzumoto, Bernice P. Bishop Museum (BPBM); Dr. Osamu Okamura, Kochi University (BSKU); Dr. Peter Last, CSIRO Marine Laboratories (CSIRO); Dr. Seishi Kimura, Mie University (FRLM); Dr. Luiz E. Pereira, Fundacao Universidade do Rio Grande (FURG); Dr. Stuart G. Poss, Gulf Coast Research Laboratory Museum (GCRL); Dr. J. -P. Gosse, Institut Royal des Sciences Naturelles de Belgique (IRSNB); Dr. Alfred Post, and Dr. Matthias Stehmann, Universitat Hamburg (ISH); Dr. Marie-Louise Bauchot, and Dr. Martine Desoutter, Muséum National d'Histoire Naturelle (MNHN); Dr. José Lima de Figueiredo, Universidade de Sao Paulo (MZUSP); Dr. Erik Åhlander, Swedish Museum of Natural History (NHRM); Dr. Martin F. Gomon, and Dr. Tarmo A. Raadik, National Museum of

Victoria (NMV); Dr. Barbara Herzig, Naturhistorisches Museum Wien (NMW); Dr. Keiichi Matsuura, National Science Museum (NSMT); Dr. Helen K. Larson, Northern Territory Museum of Arts and Sciences (NTM); Dr. Jeff Johnson, Queensland Museum (QM); Dr. D. L. Gibson, Scripps Institution of Oceanography (SIO); Dr. Friedhelm Krupp, Natur-Museum und Forschungs-Institut Senckenberg (SMF); Dr. Joseph S. Nelson, and Mr. Wayne Roberts, University of Alberta (UAMZ); Dr. George H. Burgess, University of Florida (UF); Dr. S. L. Jewett, Dr. Leslie W. Knapp, and Ms. Lisa F. Palmer, National Museum of Natural History (USNM); Dr. Theodore W. Pietsch, University of Washington (UW); Mr. Nick Haigh, and Dr. Kevin Smith, Western Australian Museum (WAM); Dr. Jorgen Nielsen, University of Copenhagen (ZMUC); and Mr. Pranesh Banerjee, Dr. R. P. Barman, Mr. Amitabha Das, Mr. Paritosh Mukherjee, and Mr. T. K. Sen, Zoological Survey of India (ZSI).

Some of the most enjoyable and memorable aspects of my graduate career at the University of Alberta included the many personal and academic benefits that I have gained through friendships with fellow officemates, John Clay Bruner, Karl W. Larsen, and Ierecê de Lucena. I hold these experiences with the deepest appreciation. Thanks a lot for all your support. I shall always remember our friendship!

I wish to express my thanks to all the graduate students I have met, especially Keqin Gao, Wolfgang Jansen, Zerina Johanson, Andre Martel, and Ken Soehn. I wish them every success in life.

I thank the staff of the Zoology office, especially Ms. Cheryl Walker, Ms. Rose Sproule, Ms. Sandy Maron, Ms. Elaine Johnston, Ms. Arlene Cowan, Ms. Jennifer Oler, late Wilma Cook, and Mr. Don Paradis for their welcoming nature and continuing support. I would also like to thank Dr. John C. Holmes, Dr. Sudarshan K. Malhotra, Dr. A. Richard Palmer, Dr. Cindy A. Paszkowski, Dr. Richard E. Peter, Dr. William M. Tonn, Mr. Randy Mandryk, Mr. Jerry Filipski, Mr. Dennis Mahood, Mr. Dean Wilson,

Mr. Nestor Lafaut, Ms. Charlotte A. Martynuik, Mr. Barry G. Bayley, Mr. Wayne E. Roberts, and Mr. Wai-Ling Wong for their encouragement and assistance in various ways. I thank Ms. Maggie Haag for coordinating teaching assignments and for her advice during my tenure as a teaching assistant. My special thanks also go to Mr. Lorne LeClair and Ms. Shyamala Nagendran for helping me in modifying the computer program for the procurement of morphometric, and meristic data and also for her assistance with so many computer snags.

I would like to take this opportunity to express my sincere gratitude to the teachers and professors I have come across over the years who inspired me to pursue a career in science, in systematics, and in ichthyology. I am grateful to all of them: late Prof. Govinda C. Banerjee, Bangabasi College; Prof. Amalesh Choudhuri, and Prof. Naresh C. Dutta, University of Calcutta; and Dr. K. C. Jayaram, Zoological Survey of India.

I wish to acknowledge the encouragement and support of Saswati Das for being a very good friend. I thank Mr. Dilip Roy and Mrs. Sumita Roy who have made my stay in Edmonton enjoyable. Debabrata Das, Tushar Pain, Kiran Pain, and many other friends deserve appreciation for providing friendship and support. Thanks to Anjan Chakravarty and Dipankar Sengupta for keeping me updated on the "homefront".

This study was financially supported by the Graduate Teaching Assistantship and Intersession Bursary provided by the Department of Zoology, and an NSERC grant to Dr. J. S. Nelson.

Finally, I would like to express my deepest gratitude to my family, especially my parents, Dr. Rabindra Nath Das, and Mrs. Renuka Das, aunt, Mrs. Kamala Bose, uncle Dr. Sunil R. Das, and aunt, Mrs. Sipra Das for the continuous source of encouragement, love and moral support.

TABLE OF CONTENTS

Chapter Page

ABSTRACT

ACKNOWLEDGMENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION....1

2. HISTORICAL ACCOUNT OF THE GENUS BEMBROPS....5

3. METHODS AND MATERIALS....8

TAXONOMIC METHODS....8

METHODS OF PHYLOGENETIC ANALYSIS....11

BIOGEOGRAPHY....14

MATERIALS....15

4. TAXONOMY OF THE GENUS BEMBROPS....16

Genus Bembrops Steindachner, 1876....16

Key to the species of Bembrops....24

Bembrops caudimacula Steindachner, 1876....28

Bembrops anatirostris Ginsburg, 1955....39

Bembrops caudimaculata Cadenat, 1937....46

Bembrops curvatura Okada and Suzuki, 1952....52

Bembrops filifera Gilbert, 1905....57

Bembrops gobioides (Goode, 1880)....62

Bembrops grevi Poll, 1959....67

Bembrops heterurus (Ribeiro, 1915).....72
Bembrops macromma Ginsburg, 1955.....78
Bembrops magnisquamis Ginsburg, 1955..... 81
Bembrops morelandi Nelson, 1978.....86
Bembrops nematopterus Norman, 1939.....90
Bembrops platyrhynchus (Alcock, 1893).....94
5. OSTEOLOGY.....100
SKULL.....100
Skull roof.....100
Ethmoid region.....109
Infraorbital series.....110
Otic and occipital regions.....111
UPPER JAW.....113
LOWER JAW.....114
SUSPENSORIUM.....115
OPERCULAR REGION.....119
HYOID ARCH.....120
BRANCHIAL ARCHES.....124
VERTEBRAE.....129
CAUDAL SKELETON AND FIN.....132
DORSAL FIN.....136
ANAL FIN.....137
PECTORAL GIRDLE AND FIN.....137
PELVIC GIRDLE AND FIN.....142

6. PHYLOGENETIC ANALYSIS.....145
MONOPHYLY OF THE GENUS.....145
INTERRELATIONSHIPS OF SPECIES OF BEMBROPS.....162
NODE II GROUP.....168
NODE III GROUP.....168
NODE IV GROUP.....175
NODE V GROUP.....179
7. BIOGEOGRAPHY.....182
TRACK ANALYSIS.....183
VICARIANCE BIOGEOGRAPHY.....185
DISPERSAL BIOGEOGRAPHY.....190
DISCUSSION.....190
8. GENERAL DISCUSSION.....196
9. LITERATURE CITED.....199
APPENDIX I.....213
APPENDIX II.....215
APPENDIX III.....218
APPENDIX IV.....221
APPENDIX V.....224

LIST OF TABLES

1.1. Classification of the family Percophidae, from Nelson (1984), pp. 341-342.....2

2.1. Summary of the taxonomic history of the genus Bembrops.....7

3.1. Data matrix for the study taxa. Plesiomorphic states are coded as '0'; apomorphic states as '1-2'. Missing data are coded as '?'.....13

4.1.1. Frequency distributions for numbers of lateral line scales of 13 species of Bembrops.....17

4.1.2. Frequency distributions for numbers of second dorsal, pectoral and anal fin rays of 13 species of Bembrops.....18

4.1.3. Frequency distributions for rows of scales between lateral line and first dorsal fin, origin of anal fin and end of anal fin of 13 species of Bembrops.....19

4.1.4. Frequency distributions for numbers of gill rakers on upper and lower limbs of branchial arch of 13 species of Bembrops.....20

4.2. Proportional measurements of Bembrops caudimacula.....29

4.3. Proportional measurements of Bembrops anatirostris.....40

4.4. Proportional measurements of Bembrops caudimaculata.....47

4.5. Proportional measurements of Bembrops curvatura.....53

4.6. Proportional measurements of Bembrops filifera.....58

4.7. Proportional measurements of Bembrops gobioides.....63

4.8. Proportional measurements of Bembrops grevi.....68

4.9. Proportional measurements of Bembrops heterurus.....73

4.10. Proportional measurements of Bembrops macromma.....79

4.11. Proportional measurements of Bembrops magnisquamis.....83

4.12. Proportional measurements of Bembrops morelandi.....87

4.13. Proportional measurements of Bembrops nematopterus.....91

4.14. Proportional measurements of Bembrops platyrhynchus.....95

7.1. Data matrix for nine distributional regions and binary codes for 13 species of Bembrops based on the phylogeny presented in Chapter 6. '?' indicates missing taxa.....188

LIST OF FIGURES

4.1. Variations in the slope of the lateral line in Bembrops.
A. Lateral line with a gradual slope; B. lateral line with an abrupt slope.....22

4.2. Geographic distribution of the genus Bembrops.....25

4.3. PCA of Bembrops caudimacula, B. curvatura, B. magnisquamis and B. nematopterus. A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....31

4.4. PCA of Bembrops caudimacula and B. magnisquamis.
A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....32

4.5. PCA of Bembrops caudimacula and B. nematopterus.
A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....33

4.6. PCA of Bembrops caudimacula and B. platyrhynchus.
A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....35

4.7. Geographic distribution of Bembrops caudimacula, B. greyi, B. magnisquamis, B. morelandi and B. nematopterus.....37

4.8. PCA of Bembrops anatirostris, B. filifera and B. gobioides.
A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....42
4.9. Geographic distribution of Bembrops anatirostris, B. caudimaculata, B. gobioides and B. heterurus.....44
4.10. PCA of Bembrops caudimaculata and B. filifera.
A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....49
4.11. PCA of Bembrops caudimaculata and B. heterurus.
A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....50
4.12. Geographic distribution Bembrops curvatura, B. filifera, B. macromma and B. platyrhynchus.....55
4.13. PCA of Bembrops greyi and B. platyrhynchus.
A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....70
4.14. PCA of Bembrops heterurus, B. macromma and B. morelandi.
A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data.....75

5.1. Left lateral view of the skull of Bembrops anatirostris.....101
5.2. Dorsal view of the skull of Bembrops anatirostris.....103
5.3. Ventral view of the cranium of Bembrops anatirostris.....105
5.4. Posterior view of the cranium of Bembrops anatirostris.....107
5.5. Internal view of the suspensorium of right side of Bembrops anatirostris.....116
5.6. Lateral view of the hyoid apparatus of left side of Bembrops anatirostris.....121
5.7. Dorsal view of the branchial apparatus of Bembrops anatirostris.....125
5.8. Left lateral view of the anterior 16 vertebrae and the dorsal fin and the anal fin skeleton of Bembrops anatirostris.....130
5.9. Left lateral view of the caudal skeleton of Bembrops anatirostris.....133
5.10. Left lateral view of the pectoral girdle (A), and postcleithra (B) of Bembrops anatirostris.....138
5.11. Ventral view (A) and left lateral view (B) of the pelvic girdle of Bembrops anatirostris.....143
6.1. Cladogram showing relationships of the four genera of the family Percophidae.....146
6.2. Ventral view of the vomer in four percophid species showing character-state distribution for Character 4 of the data matrix for the phylogenetic analysis.....148
6.3. The branchial apparatus and the hyoid apparatus of Bembrops filifera, showing character-state distribution for character 20, 32, 50 and 54 of the data matrix for the phylogenetic analysis. A. Dorsal view of the right side; B. Left lateral view.....151

6.4. The branchial apparatus and the hyoid apparatus of Percophis brasiliensis, showing character-state distribution for character 20, 32, 50 and 54 of the data matrix for the phylogenetic analysis. A. Dorsal view of the right side; B. Left lateral view.....153

6.5. Ventral view of the palatine, ectopterygoid and mesopterygoid showing character-state distribution for character 31 and 52 of the data matrix for the phylogenetic analysis. A. Chrionema chlorotaenia; B. Bembrops anatirostris.....156

6.6. Left lateral view of the urohyal showing character-state distribution for character 24 and 53 of the data matrix for the phylogenetic analysis. A. Percophis brasiliensis; B. Chrionema chlorotaenia; C. Hemerocoetes pauciradiatus; D. Bembrops anatirostris; E. B. macromma.....158

6.7. Left lateral view of the caudal skeleton showing character-state distribution for character 27, 28 and 42 of the data matrix for the phylogenetic analysis. A. Chrionema chlorotaenia; B. Bembrops gobioides; C. B. heterurus.....160

6.8. Cladogram for the relationships of the 13 species of Bembrops produced by the heuristic method (PAUP 3.0s) based on a data matrix of 54 characters.....164

6.9. Strict consensus cladogram of 13 species of Bembrops and the outgroups produced by branch and bound method (PAUP 3.0s) based on a data matrix of 54 characters.....165

6.10. Cladogram for the relationships of 13 species of Bembrops and the outgroups selected from 23 minimal length cladograms produced by branch and bound method (PAUP 3.0).....166

6.11. Cladogram for the relationships of 13 species of Bembrops showing distribution of characters for five nodes.....167

6.12. Cladogram for the relationships of seven species of Bembrops and the members of the outgroup for which data was available for all 54 characters.....169

6.13. Left lateral view of the suspensorium showing character-state distribution for character 47, 48 and 49 of the data matrix for the phylogenetic analysis.
A. Bembrops curvatura; B. B. gobioides;
C. B. filifera; D. B. platyrhynchus.....170

6.14. Cladogram showing character support for four species of Bembrops at node III of the original cladogram.....172

6.15. Dorsal view of the third hypobranchial of right side showing character-state distribution for character 51 of the data matrix for the phylogenetic analysis.
A. Percophis brasiliensis; B. Chrionema chlorotaenia; C. C. squamiceps;
D. Bembrops anatirostris; E. B. curvatura; F. B. filifera; G. B. gobioides;
H. B. heterurus; I. B. macromma; J. B. platyrhynchus.....173

6.16. Ventral view of the pelvic girdle showing character-state distribution for character 45 and 46 of the data matrix for the phylogenetic analysis.
A. Percophis brasiliensis; B. Bembrops filifera.....176

6.17. Cladogram showing character support for four species of Bembrops at node IV of the original cladogram.....178

6.18. Cladogram showing character support for five species of Bembrops at node V of the original cladogram.....180

7.1. Generalized distribution tracks of node III, IV and V species groups of Bembrops based on the available distribution data.....184

7.2. Area cladogram for the 13 species of Bembrops based on distribution data.....186

7.3. Strict consensus area cladogram for the 13 species of Bembrops based on their phylogenetic relationships using Brooks' Parsimony Analysis.....189

II.1. Truss network for species of Bembrops. Locations of 10 landmarks are illustrated as open circles and morphometric distance measures between circles as solid lines.....216

1. INTRODUCTION

The genus Bembrops belongs to the perciform family Percophidae of the suborder Trachinoidei. Members of this genus inhabit the continental shelf and slope areas from tropical to warm temperate regions of the Indo-West Pacific and Atlantic. They are found between depths of approximately 50 and 700 m. No detailed systematic study of the genus has been made, and the main literature for the genus consists of descriptions of new species, short redescriptions and reviews.

The maximum length of any species is approximately 350 mm. The species are mostly carnivorous, feeding on other smaller fishes, and some (e. g., B. heterurus) also feed on crustaceans (Knapp, 1981). These fishes are often used as fish meal.

The trachinoid family Percophidae is divided into three subfamilies and contains some 12 genera of bottom-dwelling, marine teleosts (Nelson, 1984) (Table 1.1). The systematics of the Percophidae are poorly understood as a whole, as is the case for most of the other families of the suborder Trachinoidei (Iwamoto and Staiger, 1976; Nelson, 1978; Pietsch, 1989). Nelson (1986) discussed the relationships of two trachinoid families, Trichonotidae and Creediidae, and also provided information on the morphological similarities of these two families with the percophid genus Hemerocoetes. Pietsch (1989), in his systematic study of the family Uranoscopidae, and Pietsch and Zabetian (1990), in their study of ammodytid systematics, classified Percophidae, Trichonotidae and Creediidae as a monophyletic group but did not recognize further sister groups. A detailed systematic revision of the family Percophidae is needed to resolve this trichotomy and also to achieve a well-founded classification for the family. A systematic study of the family Creediidae (by Ierecê de Lucena, a PhD student of the University of Alberta) will also help to resolve this problem.

Table 1.1. Classification of the family Percophidae, from Nelson (1984), pp. 341-342.

Order Perciformes

Suborder Trachinoidei

Family Percophidae

Subfamily Percophinae

Genus Percophis Quoy and Gaimard, 1824

Subfamily Bembropinae

Genus Bembrops Steindachner, 1876

Genus Chrionema Gilbert, 1905

Subfamily Hemerocoetinae

Genus Hemerocoetes Valenciennes, 1837

Genus Acanthaphritis Günther, 1880

Genus Pteropsaron Jordan and Snyder, 1902

Genus Osopsaron Jordan and Starks, 1904

Genus Squamicreedia Rendahl, 1921

Genus Enigmapercis Whitley, 1936

Genus Matsubaraea Taki, 1953

Genus Spinapsaron Okamura and Kishida, 1963

Genus Branchiopsaron McKay, 1971

Prior to this study, very few comprehensive studies of any genus of the family Percophidae had been attempted on a worldwide basis (see Iwamoto and Staiger, 1976; Nelson, 1979, 1982), and no detailed osteological studies were available. The present study was initiated to provide information on the phylogenetic interrelationships among the species of the percophid genus Bembrops based on detailed comparative anatomical studies. This, in turn, will provide morphological and osteological data for any future comprehensive phylogenetic study of the family.

The main objective of this study is to determine the taxonomic status and interrelationships of the species of Bembrops. This will be achieved through the following sub-objectives: 1) to revise the genus Bembrops, and provide diagnoses and complete species descriptions with information on synonymy of and distribution for each of the included species; 2) to provide a detailed osteological account of one species of the genus, B. anatirostris, and discuss the variation in a number of other species; 3) to test the hypothesis that the genus Bembrops is monophyletic and to prepare a phylogenetic hypothesis of interrelationships of all valid species of Bembrops; and 4) to analyze the patterns of geographic distribution of all the species.

The following is a brief summary of the organization of the thesis:

Chapter 2 reviews the taxonomic history of the genus.

Chapter 3 describes the different methodologies I used in the study of the taxonomy, osteology, phylogeny and biogeography of all species of Bembrops.

Chapter 4 deals with the taxonomy of each valid species. It provides synonymy, diagnostic characters, description, and distribution for the genus and for each valid species. A key to identify any specimen to one of the 13 species is also presented. Principal components analysis is used to recognize the validity of different species based on variation of morphometric, truss and meristic characters, and subjectively quantified attributes.

Short nomenclatural discussions are also given for a number of species. Information on certain biological traits including depth data is also given for all the valid species.

Chapter 5 describes the osteology of Bembrops anatirostris. Osteological characters that vary among the species of the genus and among four other percophid species used as outgroups are also discussed.

Chapter 6 focuses on the phylogenetic interrelationships of 13 valid species of Bembrops. A data matrix of 54 morphological and osteological characters is used to examine the monophyly of the genus and to present a phylogenetic hypothesis of the interrelationships of the species included in the genus. Cladistic methodology is followed to construct the phylogeny of 13 valid species using the outgroup comparison method. Cladograms are constructed using the PAUP computer program and the contributions of different characters are discussed.

Chapter 7 deals with the biogeography of 13 species of Bembrops. Dispersal biogeography, vicariance biogeography and track analysis are used to analyze the distributional patterns.

2. HISTORICAL ACCOUNT OF THE GENUS BEMBROPS

The genus Bembrops was erected by Steindachner (1876) to describe a new species, B. caudimacula, from near Nagasaki, Japan. Since then 17 more species have been described in this genus. Although Steindachner classified the genus in the family Trachinidae, Goode (1880) described B. (= Hypsicometes) gobioides from the Atlantic off Long Island, New York, and placed it in the family Merluciidae. Alcock (1893, 1894) followed Steindachner's classification, but Goode and Bean (1895) listed B. gobioides in the family Chaenichthyidae and Boulenger (1901) suggested that Bembrops should be put, with the genus Leptoscopus, in the family Leptoscopidae. Jordan and Snyder (1902) supported Boulenger's view. Gilbert (1905) placed a new species, B. filifera, in the family Pteropsaridae. Jordan and Seale (1906) placed B. filifera in Pteropsaridae following Gilbert's classification. Regan (1913), while classifying different groups within the trachinoids, placed Bembrops and its close relative Chrionema in the family Bembropsidae and considered them close to the Percophiidae (which probably then comprised only Percophis brasiliensis Quoy and Gaimard, 1825) and the Hemerocoetidae (which included Hemerocoetes and Acanthaphritis). Ribeiro (1915) was the first to use the spelling "Percophidae" while describing the new species B. (= Hypsicometes) heterurus from Brazil. Jordan (1923), in treating different groups within series Percophidiformes, included Bembrops and Chrionema in the family Pteropsaridae. Cadenat (1937), while describing fishes from the western coast of Africa, classified the genus Bembrops as a nototheniid. Fowler (1938, 1939) and Norman (1939) followed Regan's view and accepted Bembropsidae as the valid family name for the genus. Berg (1940) recognized the family Bembropidae and placed it in the superfamily Trachinoidae along with the Percophidae and Hemerocoetidae. Taki (1953) placed Bembrops along with Chrionema, Pteropsaron, Osopsaron and Matsubaraea in the family Leptoscopidae. Ginsburg (1955) made a detailed review of Regan's and Jordan's classifications of the genera and included Bembrops in the

family Percophididae. Poll (1959) followed Ginsburg. Schultz (1960), in his key to the genera related to Trichonotidae and Percophididae, classified Bembrops as a percophidid. Okamura and Kishida (1963) placed the above genera along with their new genus Spinapsaron in the family Bembropidae. Smith (1965) included Bembrops in the family Bembropsidae. Greenwood et al. (1966) synonymized the families Percophidae, Bembropsidae, Bembropidae, Pteropsaridae and Hemerocoetidae as Percophididae. Lindberg and Krasyukova (1969) recognized the family name Bembropsidae to include Bembrops. McKay (1971) divided the family Percophididae into four unnamed groups and included Bembrops and Chrionema (= Chriomystax) in one of the groups. Steyskal (1980), while dealing with the grammar of family-group names, suggested using the family name Percophidae instead of Percophididae. Nelson (1984) also recognized Percophidae as the family name and divided this taxon into three subfamilies – Percophinae, Bembropinae and Hemerocoetinae. The subfamily Bembropinae included two genera, Bembrops and Chrionema. Eschmeyer (1990) followed Nelson's classification. Table 2.1 summarizes the above mentioned information on the taxonomic history of the genus.

Table 2.1. Summary of the taxonomic history of the genus Bembrops.

Family	Genus	Species	Author(s)
Trachinidae	Bembrops	Bembrops caudimacula	Steindachner (1876)
Merluciidae	Hypsicometes	Hypsicometes gobioides	Goode (1880)
Trachinidae	Bathypercis	Bathypercis platyrhynchus	Alcock (1893)
Trachinidae	Bembrops		Alcock (1894)
Chaenichthyidae	Bembrops		Goode and Bean (1895)
Leptoscopidae	Bembrops		Boulenger (1901)
Leptoscopidae	Bembrops	Bembrops filifera	Jordan and Snyder (1902)
Pteropsaridae	Bembrops		Gilbert (1905)
Bembropsidae	Bembrops		Regan (1913)
Percophidae	Hypsicometes	Hypsicometes heterurus	Ribeiro (1915)
Pteropsaridae	Bembrops		Jordan (1923)
Nototheniidae	Bembrops	Bembrops caudimaculata	Cadenat (1937)
Bembropsidae	Bembrops	Bembrops filifer	Fowler (1938)
Bembropsidae	Bembrops	Bembrops philippinus (= Bembrops filifer)	Fowler (1939)
Bembropsidae	Bembrops	Bembrops adenensis Bembrops nematopterus	Norman (1939)
Bembropidae	Bembrops		Berg (1940)
Leptoscopidae	Bembrops		Taki (1953)
Percophididae	Bembrops	Bembrops anatirostris Bembrops macromma Bembrops magnisquamis	Ginsburg (1955)
Percophididae	Bembrops	Bembrops grevi	Poll (1959)
Percophididae	Bembrops		Schultz (1960)
Bembropidae	Bembrops	Bembrops curvatura Bembrops filodorsalia	Okamura and Kishida (1963)
Bembropsidae	Bembrops		Smith (1965)
Percophididae	Bembrops		Greenwood et al. (1966)
Bembropsidae	Bembrops		Lindberg and Krasyukova (1969)
Percophididae	Bembrops	Bembrops aethalea Bembrops indica	McKay (1971)
Percophididae	Bembrops	Bembrops morelandi	Nelson (1978)
Percophidae			Steyskal (1980)
Percophidae	Bembrops		Nelson (1984)
Percophidae	Bembrops		Eschmeyer (1990)

3. METHODS AND MATERIALS

TAXONOMIC METHODS

In the study of phylogenetic relationships, it is important to state what criteria are used to recognize a species. Speciation and the species concept have been a point of discussion for many years (Chandler and Gromko, 1989) and various criteria have been used to define species (see Mayr and Ashlock, 1991 for details). Among them, the biological species definition is the most popular and widely used. Although the biological species concept, in its true sense, cannot be employed in many taxonomic studies (e.g., reproductive isolation cannot be tested in samples of preserved specimens), morphological evidence can be used to study interrelationships among species and to infer reproductive isolation (Mayr and Ashlock, 1991). Hence, overall morphological distinction, where all specimens can be assigned to a species on the basis of separate clusters produced by the principal components analysis as explained later, was used as the basis for the recognition of species in my study of the genus Bembrops.

Some 26 traditionally used morphometric measurements, 14 meristic characters and two subjectively quantified attributes were recorded for most of the specimens. These are good descriptors of the fish and many of these characters have been used by other workers as efficient discriminators of species (Ginsburg, 1955; Nelson, 1978). Measurements and counts follow Hubbs and Lagler (1964). Atchley et al. (1976), Atchley and Anderson (1978), and Humphries et al. (1981) suggested avoiding ratios in morphometric studies because they may cause statistical errors. Therefore, log-transformed measurements were used in the morphometric analyses. Proportions of the measurements, however, were used in the species descriptions and standard length was used throughout for this purpose, so that the result could be compared with other published articles on Bembrops and other

related groups (see Nelson, 1978 and Iwamoto and Staiger, 1976). Appendix I gives details of all 42 characters. From the original 42 characters, five meristic characters (DRF1S, PELFS, PELFR, CAUDFR, and BRACSTGL) were discarded before in-depth analysis because they did not show any variation.

Many recent workers (Humphries et al., 1981; Strauss and Bookstein, 1982; Bookstein et al., 1985) have criticized the use of traditional morphometrics for describing form in systematic studies because they tend to concentrate along the horizontal axis of the body. In contrast, truss character sets using landmark points are less biased in their directional description of the body-form because, unlike the traditional measurements, they produce a more systematic geometric characterization of shape (Strauss and Bookstein, 1982). A box-truss scheme using the following landmarks was therefore also analyzed: 1) snout tip; 2) occiput; 3) origin of first dorsal fin; 4) origin of second dorsal fin; 5) end of second dorsal fin; 6, 7) hypural plate; 8, 9) anal fin base; 10) origin of pelvic fin base. Some 21 interlandmark distances were measured from these 10 landmark points. The details of 21 interlandmark distances (identified as TRUSS 1-21) are given in Appendix II.

Measurements were taken using a Mitutoyo Digital Caliper connected to an APCO Turbo PC Clone computer and a BASIC computer program developed by Limnoterra, Toronto, and modified by Lorne LeClair and Shyamala Nagendran, Department of Zoology, University of Alberta. Meristic counts and attributes were recorded with specimens under magnification using a WILD M5 stereomicroscope.

Principal components analysis (PCA) was used to identify different species based on the patterns of morphological variation. Principal components were calculated from the correlation matrix of characters using the StatView SE + Graphics™ statistical program on Macintosh computers. Calculation of principal components does not need any a priori assumptions about group (= species) membership. Phenotypically dissimilar groups can be identified from the separation of clusters in plots of principal component scores.

The analysis was conducted using a number of species that are morphologically similar together in the same data set. The analysis was conducted using the following five combinations of characters as separate data sets:

Data set 1. log-transformed morphometric measurements;

Data set 2. truss characters;

Data set 3. meristic characters and attributes;

Data set 4. log-transformed morphometric measurements, and meristic characters and attributes;

Data set 5. truss characters, and meristic characters and attributes.

The analysis showed that, because of very close morphological similarity between the species, PCA based on only log-transformed morphometric measurements or only truss characters was not a good indicator for species distinction. PCA performed with data set 3 and data set 5 was useful in identifying specimens considered to belong to different valid species. To establish the species identity, PCA scores were plotted in simple bivariate scatter plots. For the combined truss characters, and meristics and attributes data set (data set 5), the scores were plotted against the second (principal component II, PCII) and third (principal component III, PCIII) axes. An enhanced discrimination was obtained by plotting PCI of meristics and attributes data (meristic data set) against PCII of truss character data (truss data set). PCI was not used in the scatter plots for either the combined data set or the truss data set due to its high positive loading, suggesting that it represents a general size factor.

Bookstein et al. (1985) proposed "the shear: size-free discrimination" for distinguishing among groups of organisms varying in size. The sheared principal components analysis was not employed in this study because the species of Bembrops do not show any distinct variation in size.

Information on osteological characters was collected from cleared and stained specimens. Bones were stained with alizarin red and cartilage stained with alcian blue (Taylor and Van Dyke, 1985). Specimens of seven species of Bembrops were studied in detail. They were chosen because they were among the species with sufficient numbers of specimens to clear and stain. Radiographs were taken of specimens of all species of Bembrops and were used to collect information on a number of osteological characters (e.g., vertebral number, caudal skeleton, etc.). Drawings were prepared using a camera lucida attached to the WILD M5 stereomicroscope. Rojo (1991) was consulted for the nomenclature of skeletal features. Appendix III lists the abbreviations used for identification of osteological structures.

The descriptive osteology follows the general style of an osteological study of the caproid genus Antigonia (Zehren, 1987) and that of recent works on the phylogeny of uranoscopids (Pietsch, 1989), and ammodytids (Pietsch and Zabetian, 1990). Although I present a detailed description of the osteology for B. anatirostris, I discuss variable osteological characters on the basis of my examination of other taxa.

METHODS OF PHYLOGENETIC ANALYSIS

My approach to the systematic analysis of character distributions is phylogenetic (= cladistic) as described by Wiley (1981) and Mayr and Ashlock (1991, pp. 208-241). The main goal of this analysis is to discover and describe monophyletic groups by identifying shared derived character states or synapomorphies. The most challenging part of any systematic study is to determine the level of generality at which a particular character is to be considered derived.

There have been several methods, e.g., ontogeny, paleontology, outgroup analysis, etc., described to polarize character states by which synapomorphic states can be

distinguished from symplesiomorphic (shared ancestral or primitive) states (see Stevens, 1980 for details). I have used the outgroup comparison method (Watrous and Wheeler, 1981; Maddison et al., 1984) in my analysis to identify the polarity of each character. I chose four percophid species (Percophis brasiliensis, Chrionema chlorotaenia, C. squamiceps and Hemerocoetes pauciradiatus) as the members of the outgroup. Chapter 6 gives details on the criteria for choosing these species. The principle of parsimony was used to resolve situations where apomorphic characters supported conflicting hypotheses of relationship. Although the process of evolution does not proceed according to the principle of parsimony, this approach can minimize the number of assumptions to explain character transformations.

The result of a phylogenetic analysis is usually presented in a hierarchical arrangement of increasingly inclusive monophyletic groups (Charig, 1982). This arrangement, shown in a cladogram, provides the necessary hypothesis of the phylogenetic relationships of the taxa concerned.

The approach to studying the phylogeny of Bembrops was firstly to test the monophyly of the genus and secondly to ascertain which characters showed variations within the genus. A data matrix (Table 3.1) was produced based on 54 characters (see Appendix IV for a list of the characters) and was entered in the computer program PAUP Version 3.0s for the Macintosh (Swofford, 1991). All characters were entered in PAUP as unweighted and unordered. The analysis was performed in two phases. In the first phase, the data matrix was run using "heuristic" search option. "Heuristic" search is an approximate approach to search for minimum length cladograms, and takes reduced computing time. PAUP 3.0s has the option of using two basic strategies within the heuristic search – stepwise addition and branch swapping. Three algorithms are used by PAUP in the branch swapping method, among which 'nearest neighbor interchanges (NNI)' has the highest effectiveness (Swofford, 1991). I opted for the branch swapping,

Table 3.1. Data matrix for the study taxa. Plesiomorphic states are coded as '0'; apomorphic states as '1-2'. Missing data are coded as '?'. See Appendix IV and text in phylogenetic analysis section for details of characters and states.

Taxa	Characters										
	[1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-54]
	[12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	1234]
Percophis brasiliensis	11100	00000	00000	00000	00010	01100	00000	00000	00000	00000	0000
Chrionema chlorotaenia	11111	11111	00000	00011	11101	12200	00110	00101	00100	10000	0000
C. squamiceps	11111	11111	00000	00011	11101	12200	00111	10011	00100	00000	0000
Bembrops anatirostris	11111	11111	00000	00011	11101	11111	11111	10111	10110	10110	1100
B. caudimacula	11111	11111	00000	00011	11101	11111	11111	11001	1010?	?????	????
B. caudimaculata	11111	11111	00000	00011	11101	11111	11111	10001	0000?	?????	????
B. curvatura	11111	11111	00000	00011	11101	11111	11111	11102	01101	0 111	0001
B. filifera	11111	11111	00000	00011	11101	11111	11111	10111	11100	01001	0000
B. gobioides	11111	11111	00000	00011	11101	11111	11111	10102	00110	10100	1100
B. greyi	11111	11111	00000	00011	11101	11111	11111	11101	0010?	?????	????
B. heterurus	11111	11111	00000	00011	11101	11111	11111	10101	01000	00100	1011
B. macromma	11111	11111	00000	00011	11101	11111	11111	10111	00110	00100	0010
B. magnisquamis	11111	11111	00000	00011	11101	11111	11111	11001	0010?	?????	????
B. morelandi	11111	11111	00000	00011	11101	11111	11111	01111	1010?	?001?	????
B. nematopterus	11111	11111	00000	00011	11101	11111	11111	01011	1010?	?????	????
B. platyrhynchus	11111	11111	00000	00011	11101	11111	11111	11111	11101	01111	0001
Hemerocoetes pauciradiatus	11111	11111	11111	11100	00000	00000	00??1	011?0	00?0?	?1110	0?00

NNI method in the heuristic search for the minimum length cladograms. The second phase of the analysis was performed using the "branch-and-bound" search option available in PAUP. The branch-and-bound algorithm, which is used to search for the minimal tree, was first described by Hendy and Penny (1982). This method is very useful to find the globally optimal tree (Swofford, 1991). The data matrix was also run in MacClade 2.96c (Maddison and Maddison, 1988), and the values of the consistency index (a measurement which describes an inverse relationship to the degree of homoplasy) and minimum tree length were compared with the values of the trees produced by PAUP.

BIOGEOGRAPHY

During the past two decades, many biologists have paid attention to the distributional patterns of various organisms and as a result have contributed to the development of theories and methods of biogeography (Humphries and Parenti, 1986). These methods can be broadly classified into three major sets of ideas: 1) dispersal biogeography, which states that organisms could originate from one or more centers of origin and migrate to other parts of the world (Darlington, 1957; Briggs, 1984, 1987); 2) vicariance biogeography, which explains the distributional patterns of organisms by the fragmentation of a former continuous distribution of the ancestor into geographically separated areas through a barrier (Rosen, 1978; Platnick and Nelson, 1978; Nelson and Platnick, 1981; Nelson, 1985); and 3) Croizat's 'track analysis' which proposes that similarities in distribution among various taxa can lead us to the recognition of a general distributional pattern (Craw, 1982; Croizat, 1982). Vicariance method and 'track analysis' overlap with each other in many details.

The results of phylogenetic analysis in the present study have been used to discuss the distributional patterns of the species of the genus Bembrops from the points of view of all three methodologies mentioned above.

MATERIALS

Some 722 specimens of the genera Bembrops, Chrionema, Hemerocoetes and Percophis have been received on loan from 24 institutions. A list of institutions is provided in Appendix V. Institutional abbreviations follow Leviton et al. (1985).

Species accounts are provided beginning with B. caudimacula (the type species of the genus) and then proceeding in alphabetical order, beginning with B. anatirostris. Unless otherwise indicated, information on the female gonad maturity presented in the Biological Notes section was collected on the basis of my personal examination of the specimens. A detailed list of specimens examined is provided in the Materials Examined section for each species. In this section, a standard length measurement associated with a catalog number indicates that counts and measurements were taken from that specimen(s) and the data were used in the principal components analysis. All other listed materials (Other Materials Examined) were examined to confirm species identity and to establish geographical ranges. Locality information is also provided for each species.

4. TAXONOMY OF THE GENUS BEMBROPS

Family Percophidae

Genus Bembrops Steindachner, 1876

Bembrops Steindachner, 1876: 211 (type species, Bembrops caudimacula Steindachner, 1876, by monotypy).

Hypsicometes Goode, 1880: 307 (type species, Hypsicometes gobioides Goode, 1880, by monotypy).

Bathypercis Alcock, 1893: 177 (type species, Bathypercis platyrhynchus Alcock, 1893, by monotypy).

Diagnosis.-

L.L.scales 40-69; D.VI, 13-17; P.17-26; V.I, 5; A.14-18; C.11.

Bembrops is a percophid diagnosed by the following synapomorphies: presence of maxillary tentacle; presence of a deep notch at posterior tip of maxilla; presence of a median gap between two arms of palatine in the area of its articulation with mesopterygoid; wide proximal end of third branchiostegal ray; and eyes large.

Description.-

Counts of selected meristic characters for the species of Bembrops are provided in Table 4.1.

Body oblong. Head flattened, maximum width at opercular area. Lateral profile of snout somewhat convex. Upper jaw extending behind anterior margin of eye. Ascending process of premaxilla fairly long, slightly broader proximally and situated perpendicular on

Table 4.1.1. Frequency distributions for numbers of lateral line scales of 13 species of Bembrops.

Species	lateral line scales																																
	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	$\bar{X}$	SD
B. caudimacula			2	–	1	1	–	6	8	5	5	4	5	3	1																48.9	2.8
B. anatirostris																					2	–	3	8	6	1	5	4	1		64.2	2.0
B. caudimaculata																							1								62.0	–
B. curvatura	1	1	–	–	–	1	3	5	5	1																					46.3	2.4
B. filifera																					4	3	5	6	7	5	5	–	–	1	63.4	2.1
B. gobioides																					1	–	3	1	7	4	5				64.1	1.8
B. greyi													2	–	–	1															53.0	–
B. heterurus															1	–	5	2	4	5	2										57.6	1.6
B. macromma															5	5	–	4	3	3	6	3	3	2	1						58.3	3.0
B. magnisquamis						1	–	1	1	1	1																				47.8	1.9
B. morelandi																	1	–	1												57.0	–
B. nematopterus					1	1	–	–	1																						45.6	2.1
B. platyrhynchus								1	–	–	7	8	7	8	7	–	4	1													52.3	2.1

Table 4.1.2. Frequency distributions for numbers of second dorsal, pectoral and anal fin rays of 13 species of Bembrops.

Species	2nd dorsal fin rays							pectoral fin rays												anal fin rays						
	13	14	15	16	17	$\bar{X}$	SD	17	18	19	20	21	22	23	24	25	26	$\bar{X}$	SD	14	15	16	17	18	$\bar{X}$	SD
B. caudimacula	2	37	2			14.0	0.3			1	1	4	8	16	9	2		22.7	1.2	1	6	30	4		15.9	0.6
B. anatirostris		4	26			14.9	0.3							5	17	7	1	24.1	0.7				7	23	17.8	0.4
B. caudimaculata			1			15.0	–							1				23.0	–					1	18.0	–
B. curvatura		16	1			14.0	0.2			1	8	6	2					20.5	0.8		14	3			15.2	0.4
B. filifera		5	28	3		14.9	0.5						2	4	16	14		24.2	0.8			2	33	1	16.9	0.3
B. gobioides				4	17	16.9	0.2						1	2	9	8	1	24.3	0.9				4	17	17.8	0.5
B. greyi				2	1	16.3	0.6								1	2		24.7	0.6					3	18.0	–
B. heterurus		17	2			14.1	0.3	1	–	–	–	1	3	12	2			22.5	1.5			2	16	1	16.9	0.4
B. macromma		32	3			14.1	0.3						20	11	4			22.5	0.7				8	27	17.8	0.4
B. magnisquamis			4	1		15.2	0.4					1	4					21.8	0.4				5		17.0	–
B. morelandi	1	1				13.5	–									1	1	25.5	–			1	1		16.5	–
B. nematopterus	1	2				13.6	0.6					1	2					21.6	0.6			3			16.0	–
B. platyrhynchus	2	37	3	1		14.1	0.4						3	12	13	15		23.9	0.9		5	36	2		15.9	0.4

Table 4.1.3. Frequency distributions for rows of scales between lateral line and first dorsal fin, origin of anal fin and end of anal fin of 13 species of Bembrops.

Species	rows of scales between lateral line and 1st. dorsal fin							rows of scales between lateral line and origin of anal fin								rows of scales between lateral line and end of anal fin					
	2	3	4	5	6	$\bar{X}$	SD	3	4	5	6	7	8	$\bar{X}$	SD	2	3	4	5	$\bar{X}$	SD
B. caudimacula	1	39	1			3.0	0.2			4	29	8		6.1	0.5		40	1		3.0	0.2
B. anatirostris		1	24	5		4.1	0.4			7	20	3		5.9	0.6	2	24	4		3.1	0.4
B. caudimaculata			1			4.0	–					1		7.0	–			1		4.0	–
B. curvatura	13	4				2.2	0.4	3	14					3.8	0.4	3	14			2.8	0.4
B. filifera		3	31	2		4.0	0.4			1	31	4		6.1	0.4		33	3		3.1	0.3
B. gobioides			2	9	10	5.4	0.6			13	8			5.3	0.5		21			3.0	–
B. greyi	1	2				2.7	0.6			3				5.0	–		3			3.0	–
B. heterurus			1	18		4.9	0.2				11	8		6.4	0.5		12	6	1	3.4	0.6
B. macromma		24	10	1		3.3	0.5			11	19	5		5.8	0.7	4	31			2.9	0.3
B. magnisquamis	1	1	3			3.4	0.9		4	1				0.4		5				2.0	–
B. morelandi		2				3.0	–				1			6.0	–		1			3.0	–
B. nematopterus	3					2.0	–			3				5.0	–		3			3.0	–
B. platyrhynchus	13	27	2			2.7	0.5		2	36	5			5.1	0.4		42	1		3.0	0.1

Table 4.1.4. Frequency distributions for numbers of gill rakers on upper and lower limbs of branchial arch of 13 species of Bembrops.

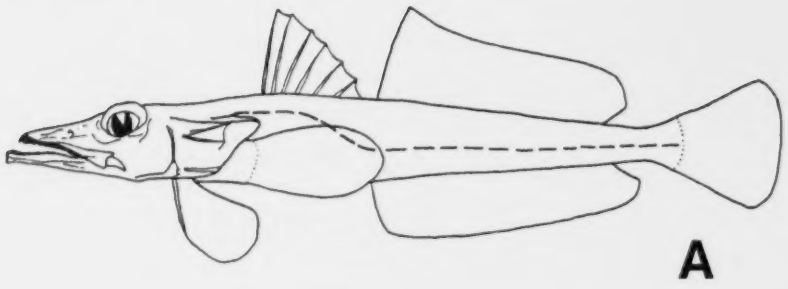
Species	gill rakers on upper lobe of branchial arch						gill rakers on lower lobe of branchial arch								
	3	4	5	6	$\bar{X}$	SD	10	11	12	13	14	15	16	$\bar{X}$	SD
B. caudimacula	3	37	1		3.9	0.3		2	5	16	8	5	5	13.7	1.3
B. anatirostris		2	10	18	5.5	0.6			2	14	13	1		13.4	0.7
B. caudimaculata				1	6.0	–					1			14.0	–
B. curvatura	12	4	1		3.3	0.6	3	6	5	3				11.5	1.0
B. filifera	2	20	13	1	4.4	0.6		2	5	12	14	3		13.3	1.0
B. gobioides			5	16	5.8	0.4			4	10	7			13.0	0.7
B. greyi			3		5.0	–		1	2					11.7	0.6
B. heterurus		2	12	5	5.1	0.6			1	7	10	1		13.5	0.7
B. macromma		12	11	12	5.0	0.8			13	18	3	1		12.8	0.7
B. magnisquamis		3	2		4.4	0.5			1	3	1			13.0	0.7
B. morelandi		2			4.0	–						2		15.0	–
B. nematopterus			3		5.0	–						1	2	15.6	0.6
B. platyrhynchus	1	34	7		4.1	0.4		4	13	19	4	2		12.7	0.9

premaxilla. Postmaxillary process of premaxilla well developed, wider at base and with rounded dorsal margin. Fine teeth on premaxilla, dentary, vomer and palatine. Maxilla toothless, exposed, with well-developed tentacle at posterior tip. Anterolateral process of maxilla directed forward but not protruding from transverse skin fold. Lower jaw protruding forward past upper jaw. Eyes large, situated high on side of head, closer to anterior end of snout than to end of opercular flap; interorbital width very narrow, flat. Two dorsal fins, first with 6 spines, second with 13-17 branched, soft rays. Last ray of second dorsal fin with two branched elements. Pectoral fin with 17-26 branched, segmented soft rays. Pelvic fin with one spine and 5 segmented, soft rays. Anal fin with 14-18 soft rays, with last 4 or 5 branched. Last ray of anal fin with two branched elements. Caudal fin with 11 branched principal rays. Dorsal procurrent rays 7-11, and ventral procurrent rays 5-9. Scales ctenoid, present on lateral and dorsal surfaces of snout, absent in gular region, present at the base of pectoral and pelvic fins. Lateral line descending gradually or abruptly in the area of pectoral fin and then running posteriorly ventral to the mid-line (Fig. 4.1). Opercle with two spines near its dorsal margin, diverging posteriorly. Subopercle with a dorsoposteriorly extending weakly ossified blade directed diagonally toward posterior tip of operculum. One spine on lower arm of subopercle. Two small spinous processes on posterior tip of posttemporal. Pseudobranchs well developed. Ceratohyal without any cirri or other internal projections. Branchiostegal rays 7. Few to numerous dark spots on caudal fin. Some 2-13 circular or oval dark blotches along lateral line.

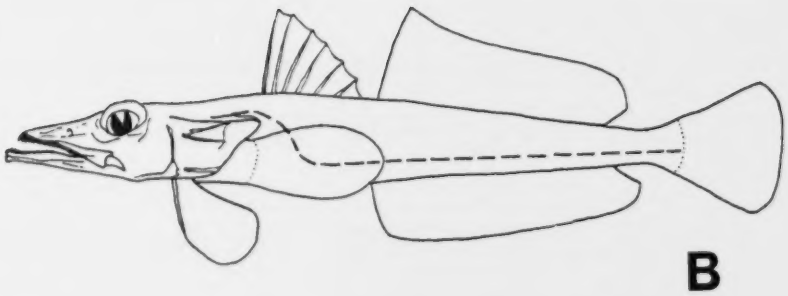
Nomenclatural Discussion.-

Steindachner (1876) erected the genus Bembrops in describing a new species, B. caudimacula, from Nagasaki, Japan. Four years later, Goode (1880) erected a new genus Hypsicometes for a new species – H. gobioides, based on a small specimen (43.5 mm SL)

Fig. 4.1. Variations in the slope of the lateral line in Bembrops. A. Lateral line with a gradual slope. B. Lateral line with an abrupt slope.



A



B

collected off the Atlantic coast of North America. In 1893, Alcock described Bathypercis platyrhynchus based on a specimen collected from the Bay of Bengal. In a subsequent publication in 1894, Alcock considered Bathypercis a junior synonym of Bembrops. Later, Alcock (1894, 1902) pointed out similarities of Bembrops with Hypsicometes and decided to synonymize both Bathypercis and Hypsicometes with Bembrops. Jordan and Snyder (1902) also supported Alcock's view.

Distribution.-

The genus is distributed throughout the Indo-West Pacific and Atlantic regions between the latitudes of approximately 40°N and 40°S (Fig. 4.2) and is found between depths of approximately 50 and 700 m.

Key to the species of Bembrops

1a. Lateral line sloping gradually..... 2

1b. Lateral line sloping abruptly..... 12

2a. Scales present in area in front of eye..... 3

2b. Scales absent in area in front of eye; 54-64 lateral-line scales; 14 or 15 rays on 2nd dorsal fin; 22-24 pectoral fin rays; 17 or 18 anal fin rays; 2nd dorsal spine elongate in some adult males..... B. macromma

3a. Lateral-line scales 42-60 (rarely 60)..... 4

3b. Lateral-line scales 60-69 (rarely less than 60)..... 10

4a Dark pigmentation on membranes between spines of 1st dorsal fin restricted to anterior four spines..... 5

4b. Dark gray to black pigmentation on membranes between all 6 spines of 1st dorsal fin..... 9

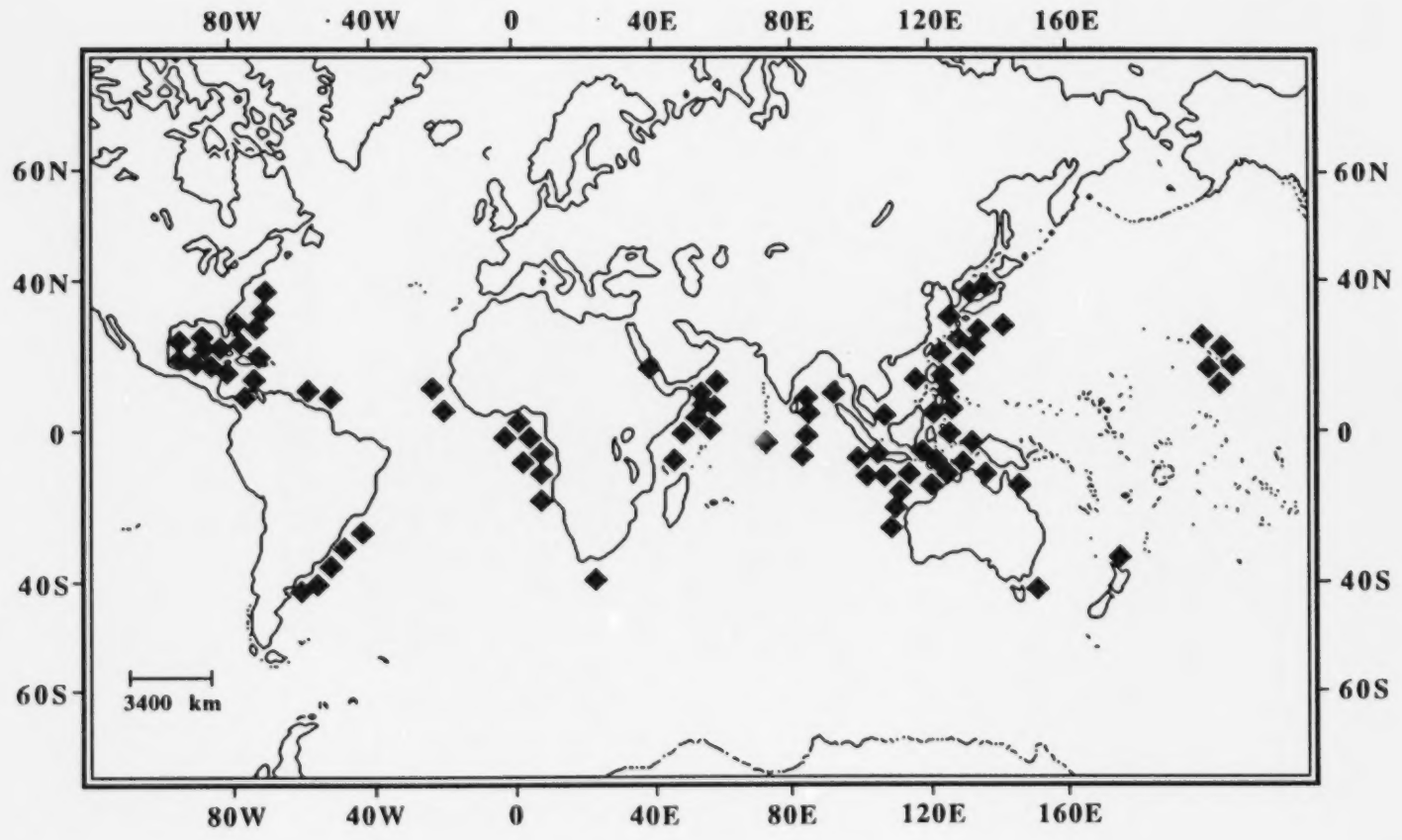


Fig. 4.2. Geographic distribution of the genus Bembrops (◆) based on data collected from original species descriptions, other literature sources, and museum collections.

5a. Maxillary tentacle long and slender, 3.5-4.0 X into length of maxilla..... 6

5b. Maxillary tentacle short and somewhat stumpy, 5.5-6.0 X into length of maxilla; upper lobe of caudal fin elongated in an acute angle; 54-60 lateral-line scales; 14 or 15 rays on 2nd dorsal fin; 17-24 pectoral fin rays; 16-18 anal fin rays..... B. heterurus

6a. Membrane between anterior 2 spines of 1st dorsal fin almost black..... 7

6b. Membrane between anterior 3 or 4 spines of 1st dorsal fin dark brown or gray..... 8

7a. Almost-black pigmentation on membrane between anterior 2 spines of 1st dorsal fin limited to distal end; lateral line with 44-48 scales; 2nd dorsal fin with 13 or 14 rays; pectoral fin with 21 or 22 rays; anal fin with 16 rays; 1st dorsal spine elongate in some young individuals..... B. nematopterus

7b. Jet black pigmentation on entire membrane between anterior 2 spines of 1st dorsal fin; lateral line with 56-58 scales; 2nd dorsal fin with 13 or 14 rays; pectoral fin with 25 or 26 rays; anal fin with 16 or 17 rays..... B. morelandi

*8a. Membrane between anterior 3 spines of 1st dorsal fin with darker pigmentation. 2nd dorsal fin with 13-15 rays (rarely 15); lateral line with 42-54 scales; pectoral fin with 19-25 rays; anal fin with 14-17 rays; ..... B. caudimacula

*8b. Membrane between anterior 4 spines of 1st dorsal fin with dark brown base. 2nd dorsal fin with 15 or 16 rays; lateral line with 45-50 scales; pectoral fin with 21 or 22 rays; anal fin with 17 rays; ..... B. magnisquamis

---

* All individuals of these two species cannot be separated in this key. Morphometric and osteological characters described in the text must be used to separate all individuals.

9a. Dark gray to black pigmentation on 1st dorsal fin confined only to dorsal edge; 47-57 lateral-line scales; 13-16 rays on 2nd dorsal fin; 22-25 pectoral fin rays; 15-17 anal fin rays; 1st dorsal spine elongate in some adult males..... B. platyrhynchus

9b. Dark gray to black pigmentation on 1st dorsal fin present on whole surface or in most part; 15-17 rays on 2nd dorsal fin; 25 pectoral fin rays; 18 anal fin rays..... B. greyi

10a. Caudal spot present..... 11

10b. Caudal spot absent; lateral line with 62 scales; 2nd dorsal fin with 15 rays; pectoral fin with 23 rays; anal fin with 18 rays..... B. caudimaculata

*11a. Caudal spot present only on dorsal edge; 1st dorsal spine elongate in adults of both sexes..... B. filifera

*11b. Caudal spot not present on dorsal edge; 2nd or 3rd dorsal spine elongate in adult males..... B. anatirostris

12a. Lateral line with 40-49 scales; 2nd dorsal fin with 14 or 15 rays; pectoral fin with 19-22 rays; anal fin with 15 or 16 rays..... B. curvatura

12b. Lateral line with 60-66 scales; 2nd dorsal fin with 16 or 17 rays; pectoral fin with 22-26 rays; anal fin with 17 or 18 rays..... B. gobioides

* All individuals of these two species cannot be separated in this key. Osteological characters described in the text must be used to separate all individuals.

Bembrops caudimacula Steindachner, 1876

Bembrops caudimacula Steindachner, 1876: 212 (Nagasaki, Japan); Alcock, 1894: 118 (Bay of Bengal, India).

Bembrops adenensis Norman, 1939: 69 (Gulf of Aden).

Diagnosis.-

L.L.scales 42-54; D.VI, 13-15; P.19-25; V.I, 5; A.14-17; C.11.

A relatively small to medium-sized member of the genus; a gradually descending lateral line (Fig. 4.1); and relatively few lateral-line scales (42-54). Distinguished from B. curvatura in having a longer snout, and a more gradually descending lateral line; and from B. nematopterus by its longer head and more scale rows between lateral line and origin of first dorsal fin (3 or 4 in B. caudimacula vs. 2 in B. nematopterus). Differentiated from B. platyrhynchus in having on average fewer lateral line scales (42-54 in B. caudimacula vs. 47-57 in B. platyrhynchus) and more scales between lateral line and origin of anal fin (5-7 in B. caudimacula vs. 4-6 in B. platyrhynchus).

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.2.

Snout moderately long. Scales present laterally and dorsally on snout including the area in front of eye. Upper jaw extending behind anterior margin of eye. Maxillary tentacle long and slender. Lateral line descending gradually adjacent to pectoral fin with 42-54 scales, separated from origin of anal fin by 5-7 rows of scales and from end of anal fin by 3 or 4 rows of scales. Scales between lateral line and first dorsal fin in 3 or 4 rows.

Table 4.2. Proportional measurements of Bembrops caudimacula (n = 41) (expressed as thousandths of standard length).

CHARACTERS	HOLOTYPE	MEAN (RANGE)	SD
HDL	408	425.9 (380-485)	24.3
HDW	144	157.7 (128-218)	18.7
HDH	97	112.9 (92-154)	14.0
EYD	90	103.3 (85-154)	15.9
SNL	124	136.0 (123-195)	14.1
POL	190	201.6 (157-285)	25.8
TNTL	39	45.1 (23-83)	15.9
UPJL	142	156.2 (140-204)	10.7
BDD	103	130.9 (103-199)	18.6
PRDR1	385	411.7 (379-441)	16.1
PRDR2	542	573.3 (538-598)	17.1
PSDR1	506	507.6 (446-548)	22.2
PSDR2	105	124.6 (104-147)	11.2
PECFL	197	230.1 (197-261)	16.9
INPECD	120	125.0 (91-156)	17.1
PELFL	178	166.4 (149-186)	10.7
INPELD	151	72.9 (53-151)	14.9
IOW	12	11.0 (6-23)	3.4
LCPD	100	107.4 (87-153)	13.3
HCPD	56	58.1 (45-70)	5.4
DRFNB1	124	108.9 (83-134)	10.8
DRFNB2	348	331.1 (296-365)	17.5
ANLFNB	343	340.5 (316-374)	14.1
ANSANL	47	33.3 (19-52)	7.9

Dorsal fin VI, 13-15. No prolongation of any dorsal spines. Predorsal length for first dorsal fin almost equal to head length. Pectoral fin rounded at outer edge and with 19-25 branched rays. Anal fin with 14-17 rays. Caudal fin rounded. Gill rakers 3-5 on upper limb of branchial arch and 11-16 on lower limb.

Color in Alcohol.-

Yellowish brown dorsally, lighter ventrally. Scales with dark brown edge. A series of 4-12 oval or circular dark brown spots along the lateral line. Membranes between first three spines of first dorsal fin dark gray to black. Caudal fin with dark pigment running along its dorsal edge and a round patch below mid-line. Peritoneum grayish to light yellowish brown, with scattered dark spots in some specimens. Norman (1939) noted "some small scattered yellowish-green markings on head and body."

Remarks.-

B. caudimacula was compared to B. curvatura, B. magnisquamis, B. nematopterus and B. platyrhynchus using PCA. The scatter plots (Fig. 4.3) show that specimens of B. caudimacula are separated distinctly from B. curvatura, but that B. caudimacula is morphologically similar to B. magnisquamis and B. nematopterus when they are analyzed together with B. curvatura. The position of the anal fin relative to that of the dorsal fin and its length, the slope of the lateral line, and the color of the peritoneum are important in the combined data set, whereas the slope of the lateral line, scales between the first anal fin ray and the lateral line, and the color of the peritoneum are important in the meristic data set in discriminating B. curvatura from the other three species.

Pairwise PCA's were performed to compare the morphology between B. caudimacula and B. magnisquamis, and between B. caudimacula and B. nematopterus. The results (Figs. 4.4 and 4.5) show a distinct separation of the B. caudimacula cluster

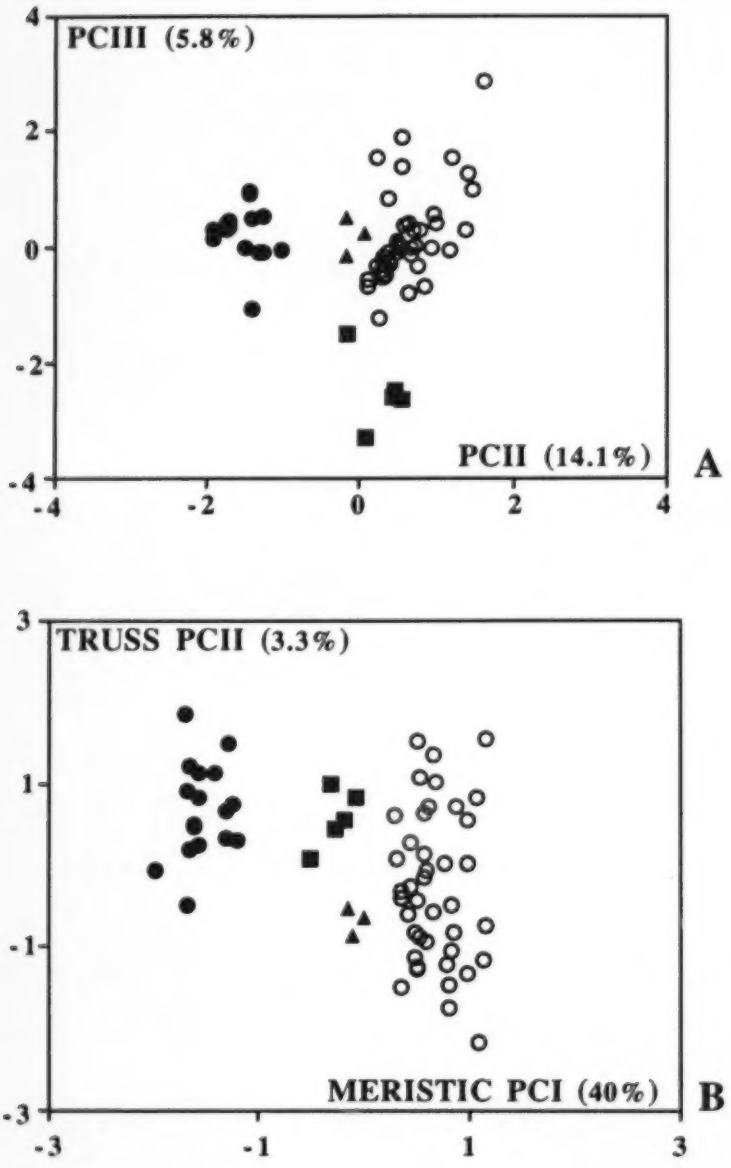


Fig. 4.3. PCA of B. caudimacula (o), B. curvatura (●), B. magnisquamis (■) and B. nematopterus (▲). A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data. Variance explained by each factor is given in parentheses.

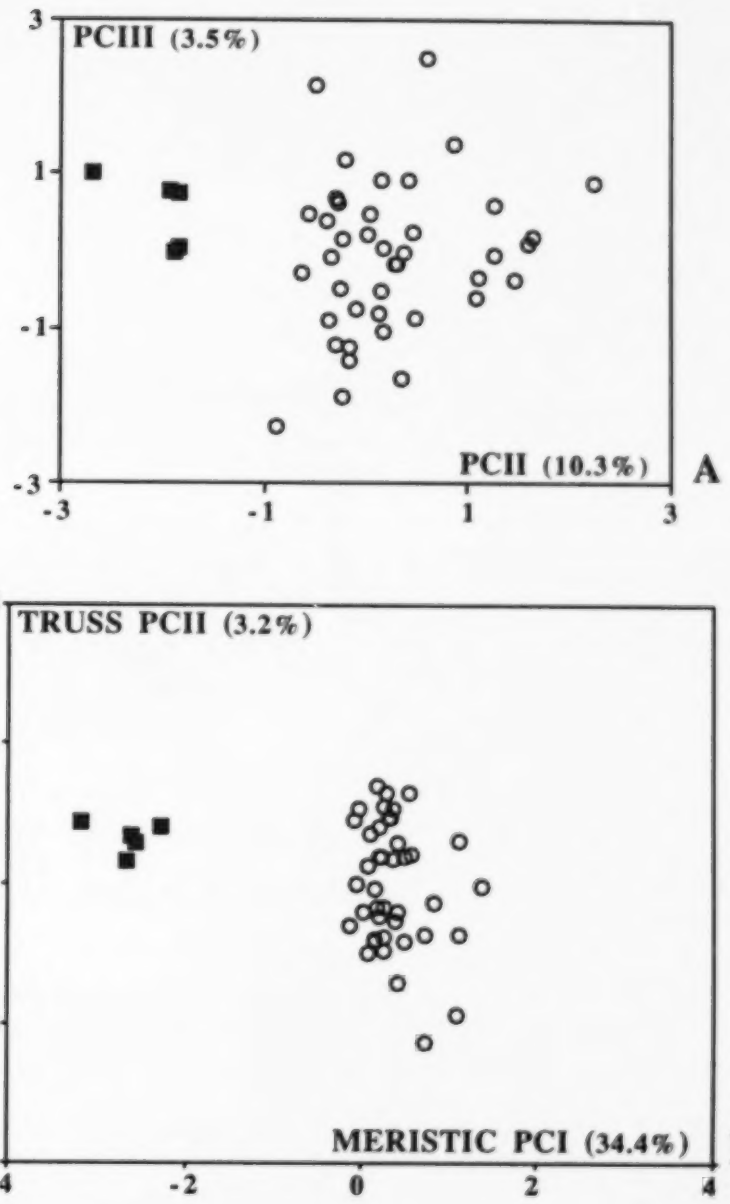


Fig. 4.4. PCA of B. caudimacula (o) and B. magnisquamis (■). A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII truss data. Variance explained by each factor is given in parenrtheses.

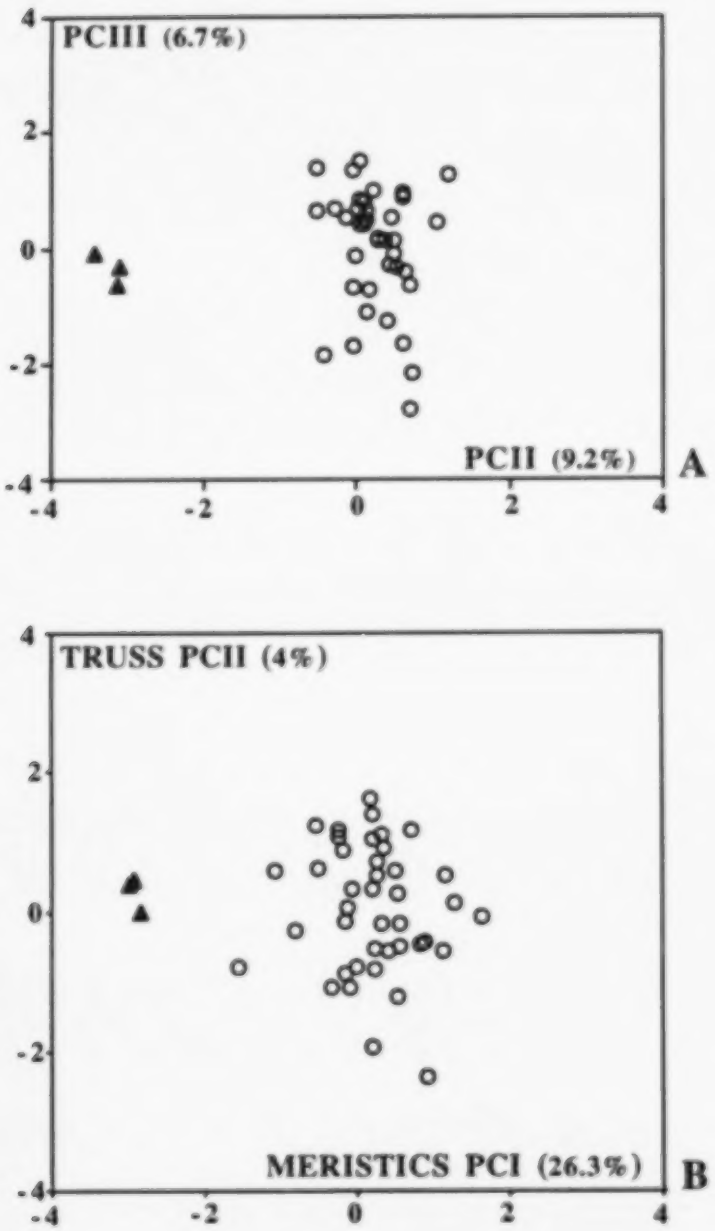


Fig. 4.5. PCA of B. caudimacula (o) and B. nematopterus (▲). A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data. Variance explained by each factor is given in parentheses.

from that of B. magnisquamis and B. nematopterus. The length of the second dorsal fin and the number of fin rays in the second dorsal fin and the anal fin are the three most important characters in the combined data set, while the second dorsal fin ray number, and scales between the last anal fin ray and the lateral line are important in the meristic data set in distinguishing between B. caudimacula and B. magnisquamis. Distance between end of second dorsal fin and end of anal fin, and scale rows between lateral line and origin of first dorsal fin are important in the combined data set, and gill rakers on upper limb and scales between first dorsal fin spine and lateral line are important in the meristic data set for distinguishing B. caudimacula from B. nematopterus.

Bembrops caudimacula also closely resembles B. platyrhynchus. My study suggests that the two species are similar on the basis of the characters used in the morphometric analyses. Although their morphometric characters do not show any marked difference, some meristic characters are important in distinguishing most specimens of the two species (Fig. 4.6). The number of scales between the lateral line and origin of the anal fin has the highest factor loading among the characters of the meristic data set. Pigmentation on the membranes between the spines of the first dorsal fin, which was not used in the PCA, proves to be a distinguishing character for the identity of the two species. A number of osteological characters also show differences. A detailed discussion of these characters is presented in Chapter 6.

Nomenclatural Discussion.-

Steindachner (1876) described Bembrops caudimacula based on a single specimen from Nagasaki, Japan, and erected the genus Bembrops. Smith (1965) considered B. platyrhynchus, B. adenensis and B. nematopterus as synonyms of B. caudimacula. Alcock (1899, 1902) and Kuroda (1950) also listed B. platyrhynchus and B. gobioides as synonyms of B. caudimacula. At my request, the holotype of B. caudimacula was

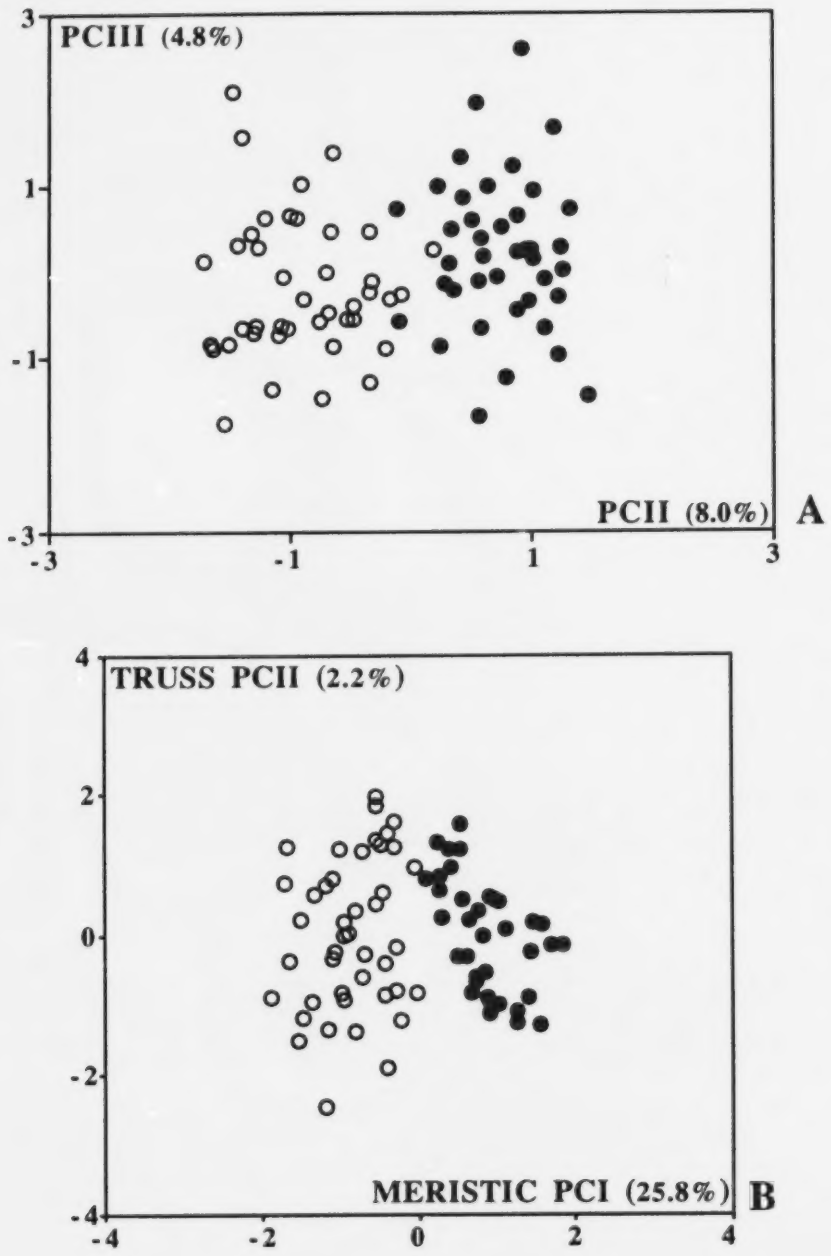


Fig. 4.6. PCA of B. caudimacula (o) and B. platyrhynchus (●). A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data. Variance explained by each factor is given in parentheses.

examined by Barbara Herzig, Curator of Fishes at the Naturhistorisches Museum Wien, Austria. This specimen has the lowest number of lateral line scales for the species. I have examined the type specimens of B. adenensis, B. nematopterus and B. platyrhynchus. In the original description of B. adenensis, Norman (1939) recognized the close resemblance of the two species, with the exception of the head and snout length and the lateral line scales. B. caudimacula demonstrates considerable variation in the number of lateral line scales (42-54) due to its wide geographic distribution. I support Smith's view of synonymizing B. adenensis with B. caudimacula.

Distribution.-

Known from the Indo-West Pacific from Japan and Korea, south to Borneo and northeastern Australia west to the Andaman Sea and Indian Ocean, and in the Gulf of Aden and Red Sea; the eastern Atlantic only in the Gulf of Guinea (Fig. 4.7).

Biological Notes.-

A relatively deep water species occurring at depths of 250 to about 500 m. Female specimens with ripe ova collected in March and May.

Etymology.-

The specific name is derived from the Latin cauda, meaning tail, and macula, meaning spot or stain, and refers to the dark blotch on the dorsal edge of the caudal fin.

Materials Examined.- (41 specimens, 76.6 – 177.0 mm in SL).

NMW 6458, 1: 116.5 mm SL (holotype), Nagasaki, Japan; BMNH 1939.5.24:1232-71, 5: 112.4-147.3 mm SL (paratypes of Bembrops adenensis), Gulf of Aden; BSKU 17632-17636, 5: 142.7-163.8 mm SL, South China Sea (07°26'N,

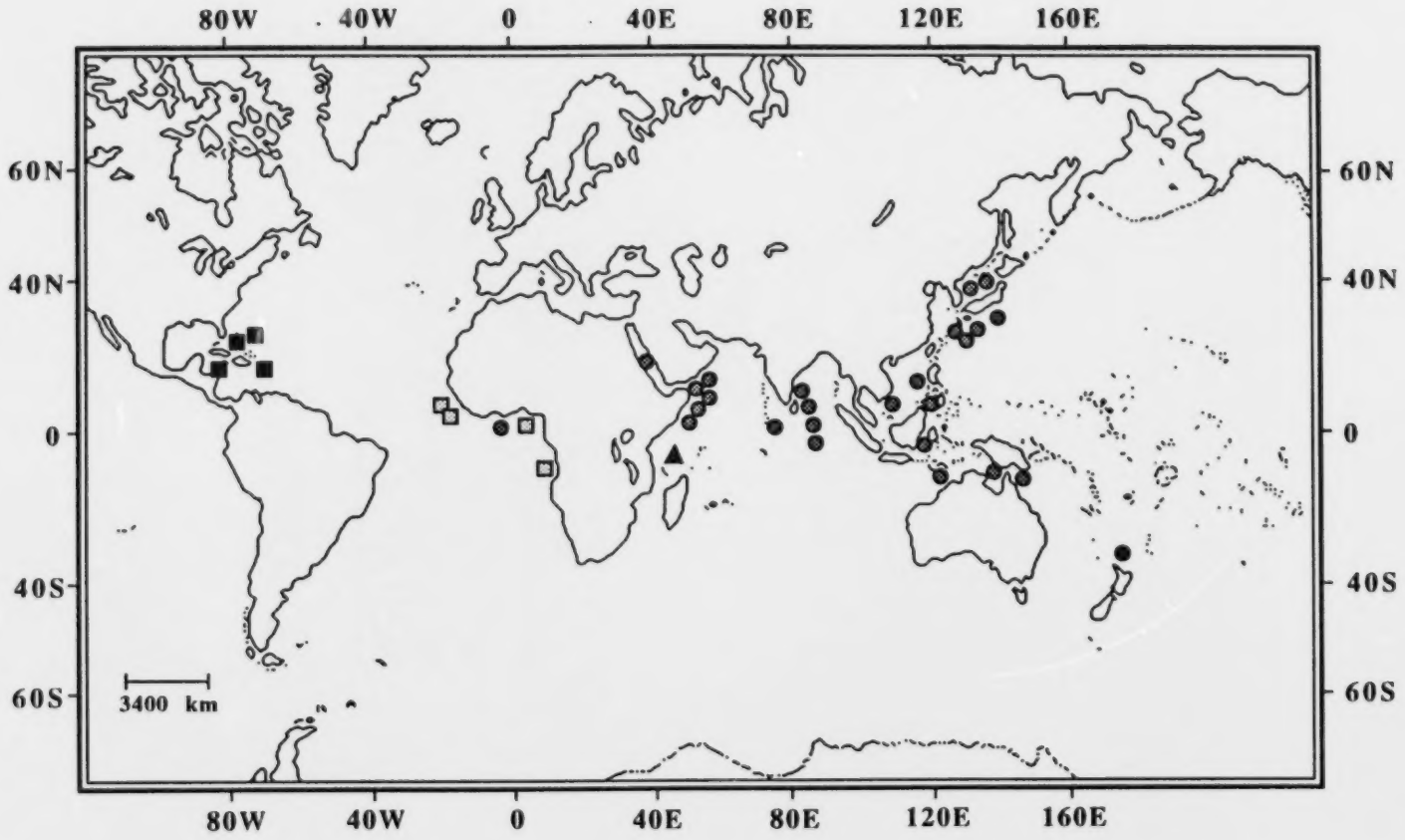


Fig. 4.7. Geographic distribution of B. caudimacula (●), B. greyi (⊡), B. magnisquamis (■), B. morelandi (●), and B. nematopterus (▲) based on data collected from original species descriptions, other literature sources, and museum collections.

109°15'E); QM I.20655, 2: 106.7-163.7 mm SL, east of Murray Isles, northern Queensland, Australia (09°53'S, 144°23'E); QM I.22339, 2: 133.4-175.6 mm SL, North West Shelf, Australia (18°21'S, 117°56'E). SMF 15386, 1: 142.2 mm SL, Rotes Meer, southwest Ras Abu Shagara, Sudan (20°54'N, 37°26'E); SMF 15387, 1: 89.9 mm SL, Zentr. Rotes Meer (21°22'N, 39°04'E); SMF 15388, 3: 76.6-96.7 mm SL, Zentr. Rotes Meer (21°22'N, 39°04'E); ZSI F257/1, 1: 115.1 mm SL, Andaman Sea; ZSI F373/1, 1: 177.0 mm SL, Andaman Sea; ZSI F673/1-F676/1, 4: 124.3-168.3 mm SL, Gulf of Manar; ZSI F6300/2, 10: 78.8-164.4 mm SL, off Quillon, Kerala, India; ZSI F7194/2, 5: 134.0-145.0 mm SL, off Quillon, Kerala, India.

Bembrops anatirostris Ginsburg, 1955

Bembrops anatirostris Ginsburg, 1955: 635 (Gulf of Mexico, east of Mississippi Delta).

Diagnosis.-

L.L.scales 60-68; D.VI, 14-15; P.23-26; V.I, 5; A.17-18; C.11.

A relatively large member of the genus; gradually sloping lateral line with relatively high number of lateral-line scales (60-68); elongate second or third spine of first dorsal fin in large males. A member of the anatirostris species group (with gobioides, caudimaculata, and heterurus) defined by the extended anterior end of the third hypobranchial. Differs from B. filifera in having dorsal fins more posteriorly inserted, and more anal fin rays (18 in 77% of B. anatirostris specimens vs. 17 in 96% of B. filifera specimens). Distinguished from B. gobioides in number of second dorsal fin rays (15 in 87% of B. anatirostris specimens vs. 17 in 93% of B. gobioides specimens).

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.3.

Snout moderately long. Scales on lateral and dorsal sides of snout. Upper jaw extending behind anterior margin of eye but not reaching its mid-line. Maxillary tentacle long and slender. Lateral line descending gradually in the area of pectoral fin with 60-68 scales, separated from origin of first dorsal fin by 3-5, from origin of anal fin by 5-7, and from end of anal fin by 2-4 rows of scales. Dorsal fin VI, 14-15. Larger males (SL > 170 mm) with elongated second or third spine of first dorsal fin. Predorsal length for first dorsal fin almost equal to head length. Pectoral fin more or less rounded at its outer edge

Table 4.3. Proportional measurements of Bembrops anatirostris (n = 30) (expressed as thousandths of standard length).

CHARACTERS	HOLOTYPE	MEAN (RANGE)	SD
HDL	419	388.1 (350-419)	14.7
HDW	136	140.8 (123-160)	9.4
HDH	107	107.6 (95-126)	7.8
EYD	92	88.5 (78-106)	5.7
SNL	150	136.6 (123-159)	10.1
POL	182	171.5 (151-195)	8.1
TNTL	64	52.1 (29-66)	8.4
UPJL	152	145.4 (137-160)	5.4
BDD	127	130.3 (110-158)	12.8
PRDR1	421	400.0 (378-421)	11.7
PRDR2	582	556.8 (523-582)	15.6
PSDR1	514	523.1 (500-552)	13.8
PSDR2	115	124.3 (101-146)	9.7
PECFL	246	231.5 (200-252)	12.2
INPECD	132	124.6 (84-157)	15.8
PELFL	151	148.5 (137-159)	5.2
INPELD	73	66.9 (56-80)	5.5
IOW	9	8.7 (7-12)	1.0
LCPD	85	102.1 (81-140)	12.2
HCPD	50	46.7 (39-51)	2.7
DRFNB1	115	104.9 (90-124)	7.5
DRFNB2	357	343.8 (315-374)	13.5
ANLFNB	356	368.7 (343-394)	14.5
ANSANL	28	35.1 (26-45)	4.9

with 23-26 branched rays. Anal fin with 17-18 rays. Caudal fin emarginate with upper lobe slightly larger than lower lobe in some specimens, two lobes of equal length in others. Gill rakers 4-6 on upper limb and 12-15 on lower limb of branchial arch.

Color in alcohol.-

Yellowish brown dorsally, lighter ventrally. Scales with darker edge. Series of 5-10 dark spots along lateral line, relatively indistinct in larger specimens. Membranes between first three or four spines of first dorsal fin darker; posterior edge of elongated spine also darker. Spots on caudal fin indistinct. Peritoneum black.

Remarks.-

Ginsburg (1955) noted the close resemblance of B. anatirostris to B. gobioides, and Grey (1959) mentioned its close similarity to B. filifera. The species was compared with B. filifera and B. gobioides using PCA. Scatter plots of PCII vs. PCIII of the combined data set, and meristic PCI vs. truss PCII (Fig. 4.8) plots suggest that B. anatirostris is morphologically more similar to B. filifera than to B. gobioides. The three species are separated on the PCII axis in the combined data set. The number of second dorsal fin rays, the number of scale rows between the lateral line and origin of first dorsal fin, and the number of anal fin rays contributed most in their separation. The color of the peritoneum and the number of gill rakers on the upper limb of branchial arch have the highest factor loadings on PCIII. Both the meristic PCI and the truss PCII are important in species discrimination. The distance between the ventral hypural plate and the posterior base of the anal fin (Truss 8), and the number of anal fin rays contributed most in these two analyses.

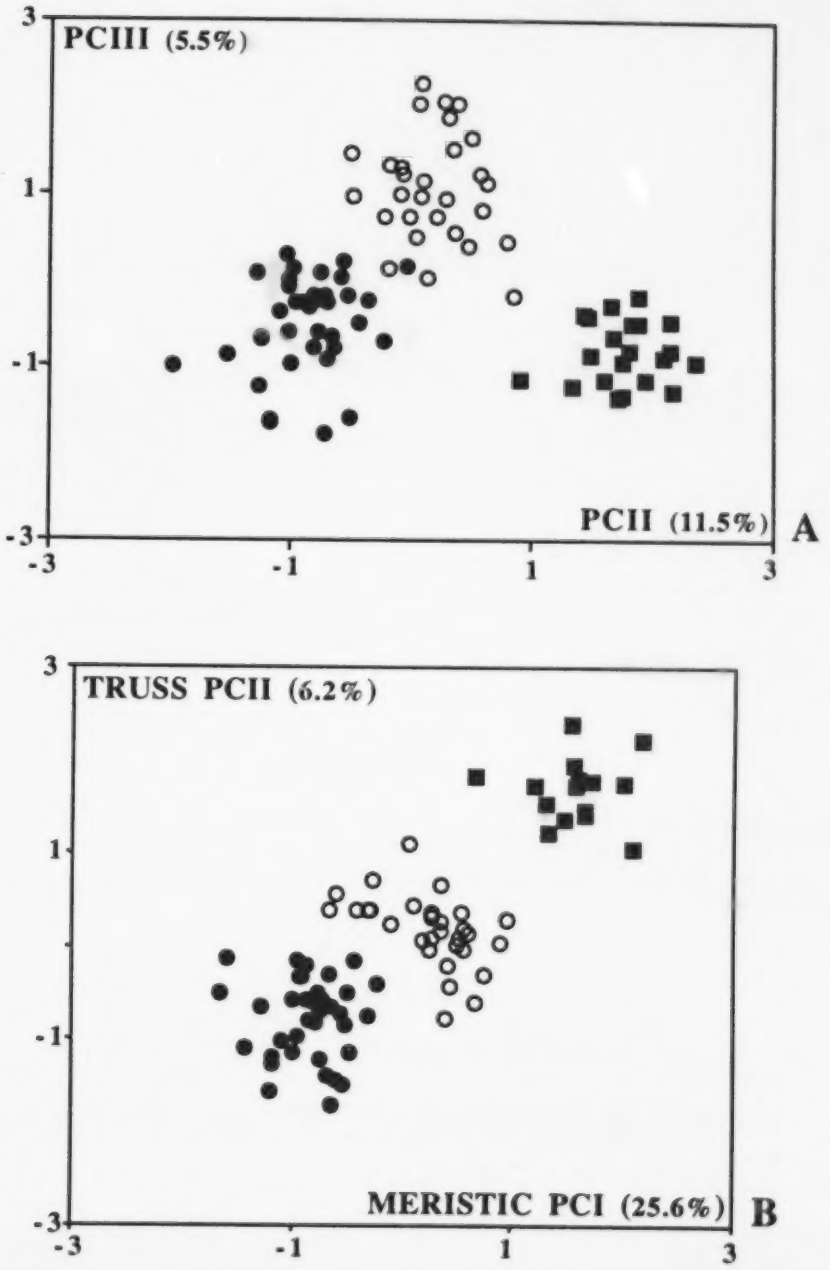


Fig. 4.8. PCA of B. anatirostris (o), B. filifera (●) and B. gobioides (■). A. Scatter plot of PCII and PCIII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data. Variance explained by each factor is given in parentheses.

Distribution.-

Western Atlantic from the Gulf of Mexico, Caribbean Sea off Puerto Rico, Suriname, and French Guiana (Fig. 4.9).

Biological Notes.-

Known from depths of 100 to over 350 m. Female specimens collected in January, February, April and May have ripe eggs. Richards (1990) illustrates several larval stages of this species. Caudal and pectoral fins appear at the 2.0 mm SL stage. All fins and the maxillary tentacles are prominent at the 9.4 mm SL stage. Pigmentation appears first at the base of the pectoral fin and on side in front of caudal peduncle.

Etymology.-

The specific name is derived from the Latin anatinus, meaning duck's, and rostrum, meaning beak or snout, and refers to the flattened duck-bill like snout.

Materials Examined.- (30 specimens, 113.0 – 262.0 mm in SL).

USNM 155470, 1: 229.7 mm SL (holotype), Gulf of Mexico, east of Mississippi Delta (29°02'N, 88°40'W); USNM 157734, 1: 146.0 mm SL (paratype), Florida off Tampa (28°10'N, 85°00'W); USNM 157735, 4: 198.0-262.0 mm SL (paratypes), off Cape San Blas, Florida (28°41'N, 86°03'W); USNM 157736, 5: 114.7-219.0 mm SL (paratypes), off Pensacola, Florida (29°20'N, 87°42'W); USNM 157737, 5: 190.5-251.0 mm SL (paratypes), Gulf of Mexico, Florida; USNM 157740, 1: 141.7 mm SL (paratype), Florida off Pensacola (30°03'N, 86°56'W); UF 20747, 13 :113.0-176.4 mm SL, Gulf of Mexico, off Florida (29°16'N, 86°05'40"W).

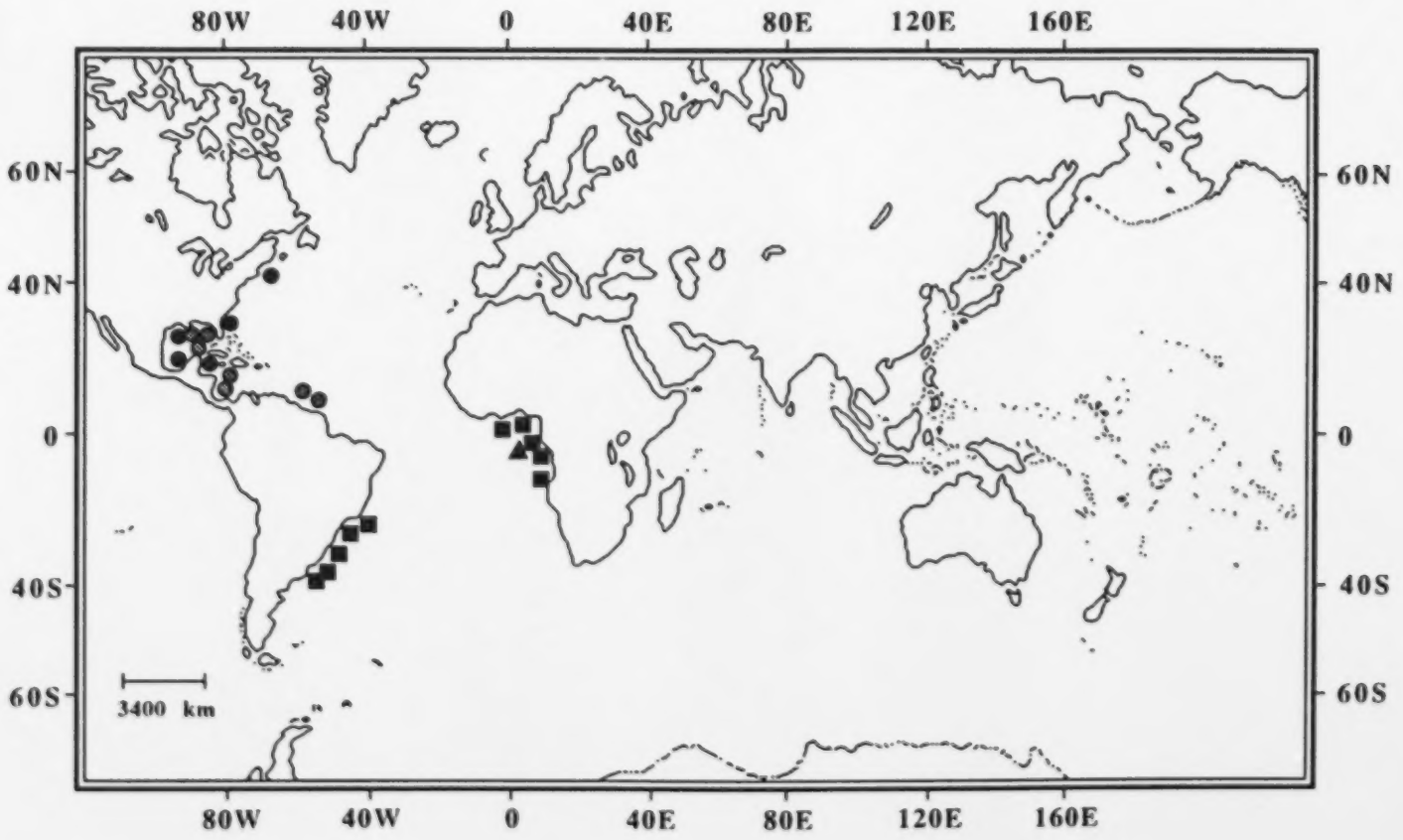


Fig. 4.9. Geographic distribution of B. anatirostris (●), B. caudimaculata (▲), B. gobioides (●), and B. heterurus (■) based on data collected from original species descriptions, other literature sources, and museum collections.

Other Materials Examined.-

USNM 44609, 1 (paratype), Gulf of Mexico, Florida (28°36'N, 85°33'W); USNM 45976, 1 (paratype), Gulf of Mexico, Louisiana (29°14'N, 88°09'W); NSMT P44756, 7, Caribbean Sea (07°32'N, 54°06'W); USNM 231943, 2, West Indies (15°38'N, 61°15'W); USNM 304913, 5, Caribbean, Nicaragua (12°26'N, 82°24'W); USNM 304914, 3, Gulf of Mexico, Louisiana (27°54'N, 90°04'W); USNM 304915, 6, Caribbean, Jamaica (17°53'N,77°56'W); USNM 304916, 2, Atlantic, Florida (29°03'N, 80°00'W).

Bembrops caudimaculata Cadenat, 1937

Bembrops caudimaculata Cadenat, 1937: 513 (off coast of Guinea, Africa, erroneous spelling of caudimacula); Norman, 1939: 69; Poll, 1959: 39 (misidentified as B. heterurus); Nelson, 1978: 240.

Diagnosis.-

L.L.scales 62; D.VI, 15; P.23; V.I, 5; A.18; C.11.

A species of Bembrops with following combination of characters (based on only known specimen): 62 lateral-line scales, 4 scale-rows between lateral line and origin of first dorsal fin, and 4 scale-rows between lateral line and end of anal fin. Distinguished from B. heterurus in number of anal fin rays (18 vs. 17 in 84% of specimens of B. heterurus).

Description.-

Nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) for the holotype are given in Tables 4.1 and 4.4.

Snout relatively short. Scales present laterally and dorsally on snout. Upper jaw extending behind anterior margin of eye but not reaching its mid-line. Maxillary tentacle medium-sized, slender. Lateral line descending gradually in the area of posterior third of pectoral fin with 62 scales, separated from origin of first dorsal fin by 4 rows of scales, from origin of anal fin by 7 rows of scales and from end of anal fin by 4 rows of scales. Dorsal fin VI, 15; no evidence of prolongation of any spine of first dorsal fin. Predorsal length for first dorsal fin slightly higher than head length. Pectoral fin relatively pointed at its outer edge with 23 branched rays. Anal fin with 18 rays. Caudal fin truncate; no prolongation of rays of upper lobe. Gill rakers 6 on upper limb and 14 on lower limb of branchial arch.

Table 4.4. Proportional measurements of Bembrops caudimaculata (n = 1) (expressed as thousandths of standard length).

CHARACTERS	HOLOTYPE
HDL	373
HDW	153
HDH	109
EYD	87
SNL	122
POL	167
TNTL	39
UPJL	136
BDD	122
PRDR1	379
PRDR2	533
PSDR1	545
PSDR2	133
PECFL	222
INPECD	127
PELFL	158
INPELD	66
IOW	10
LCPD	110
HCPD	54
DRFNB1	116
DRFNB2	347
ANLFNB	393
ANSANL	33

Color in Alcohol.-

Yellowish brown dorsally, lighter ventrally. Scales with dark brown edge. A series of 7 or 8 very indistinct spots along the lateral line. Membrane between first and second spines of first dorsal fin dark gray. Cadenat (1937) reported presence of a distinct caudal spot, but it is absent in the holotype. Peritoneum dark gray.

Remarks.-

PCA was performed using the combined data set and the truss and meristic data set to summarize the morphological differences among B. caudimaculata, B. filifera, B. heterurus, and B. macromma. The results of the pair-wise PCA's with B. caudimaculata and B. filifera specimens (Fig. 4.10) show that the two species can be separated using both data sets. In the combined data set, the number of scale-rows between the lateral line and the end of the anal fin, and the color of the peritoneum have the highest loadings on PCII, and the gill rakers on the upper limb of the branchial arch and the number of the anal fin rays on PCIII. The distance between the ventral hypural plate and the posterior base of the anal fin (Truss 8), and the number of scales between the first anal fin ray and the lateral line have the highest loadings in the truss and the meristic data set. B. caudimaculata can also be separated from B. macromma and B. heterurus on PCII of the combined data set, primarily because of the number of scale-rows between the lateral line and the origin of the first dorsal fin, the number of the anal fin rays, and the number of scale-rows between the lateral line and the end of the anal fin (Fig. 4.11). The meristic PCI was also important in the discrimination and has the highest loadings in the number of scales between the first dorsal fin spine and the lateral line (Fig. 4.11).

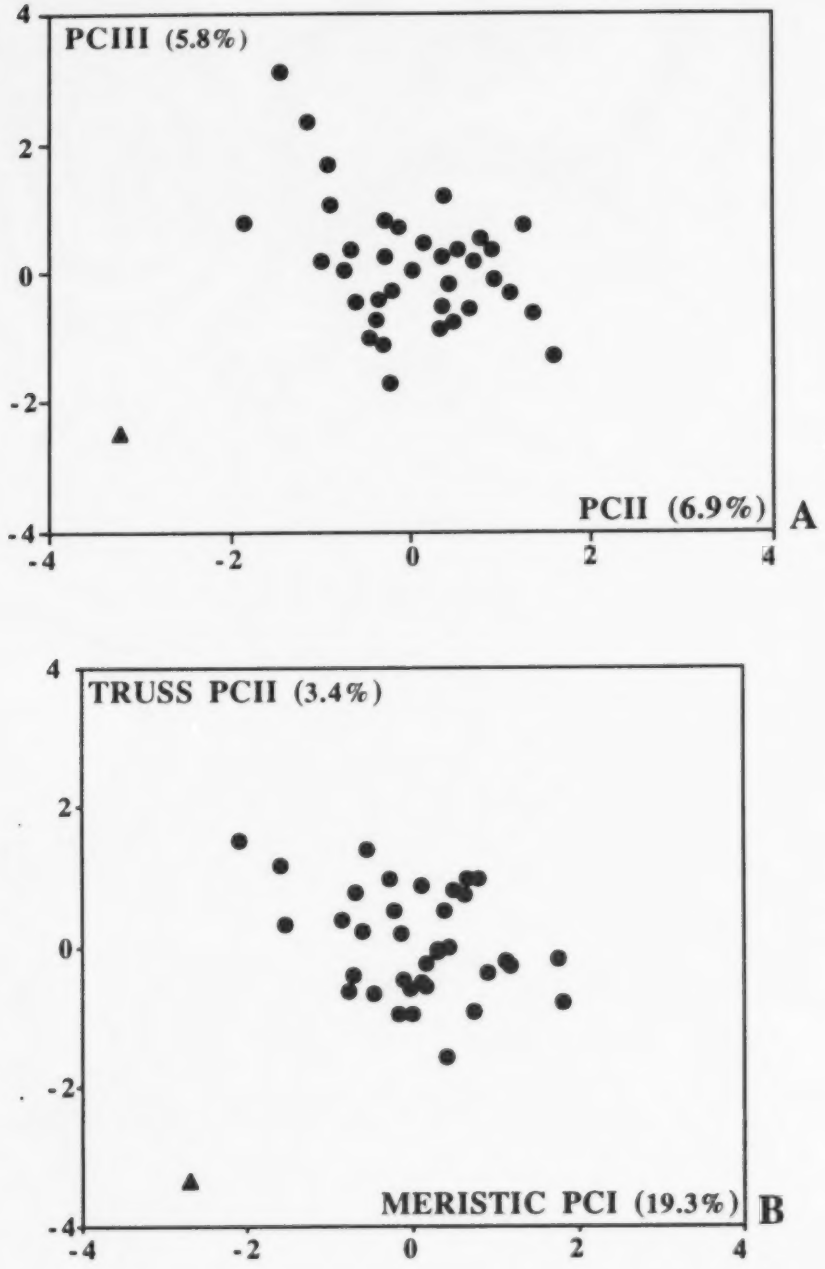


Fig. 4.10. PCA of B. caudimaculata (▲) and B. filifera (●). A. Scatter plot of PCII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data. Variance explained by each factor is given in parentheses.

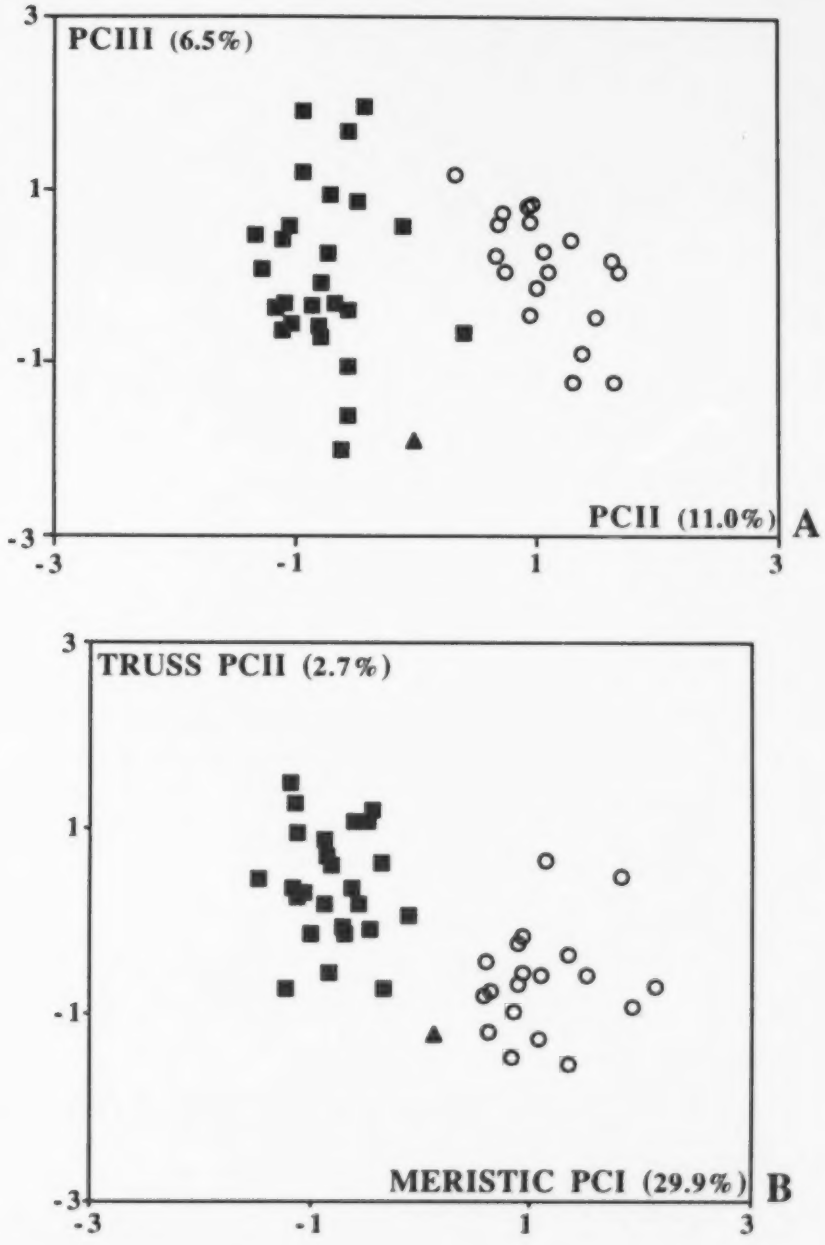


Fig. 4.11. PCA of B. caudimaculata (▲), B. heterurus (○) and B. macromma (■). A. Scatter plot of PCII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data. Variance explained by each factor is given in parentheses.

Nomenclatural Discussion.-

Cadenat (1937) erroneously identified a number of specimens from the Gulf of Guinea as B. caudimaculata Steindachner, 1876 (erroneous spelling of the specific name caudimacula) and further considered it synonymous with Hypsicometes gobioides Goode, 1880, Bathypercis platyrhynchus Alcock, 1893, and H. heterurus Ribeiro, 1915. Norman (1939) designated it as a separate species in a footnote (p. 69). Poll (1959), after examining two specimens of B. caudimaculata received from Cadenat, considered it synonymous with B. heterurus. Nelson (1978) referred to this in his short descriptions of different species of Bembrops. My comparison of the holotype of B. caudimaculata with other species suggests that it should be recognized as a separate species.

Distribution.-

Eastern Atlantic in the Gulf of Guinea (Fig. 4.9).

Biological Notes.-

The holotype was from a depth of 120 m; it came from samples collected at depths between 120 and 220 m.

Etymology.-

The specific name resulted from an erroneous spelling of caudimacula.

Materials Examined.- (one specimen, 164.3 mm in SL).

MNHN 1938-17, 1: 164.3 mm SL (holotype), off coast of Guinea, Africa.

Bembrops curvatura Okada and Suzuki, 1952

Bembrops curvatura Okada and Suzuki, 1952: 68 (Owashi, Mie Prefecture, Japan).

Diagnosis.-

L.L. scales 40-49; D.VI, 14-15; P.19-22; V.I, 5; A.15-16; C.11.

A relatively small member of the genus; lateral line descending abruptly over pectoral fin. Distinguished from B. caudimacula, B. magnisquamis and B. nematopterus by the presence of very light colored peritoneum and relatively sharp curvature of the lateral line. Distinguished from B. gobioides in counts of lateral-line scales (60-66 in B. gobioides), second dorsal fin rays (16-17 in B. gobioides), and anal fin rays (17-18 in B. gobioides).

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.5.

Snout short. Scales on lateral and dorsal sides of snout. Upper jaw extending beyond anterior margin of eye but not reaching the mid-line. Maxillary tentacle short and slender. Eyes moderate in diameter. Lateral line descending rather abruptly after a gradual upward slope for two scale-rows from origin; with 40-49 scales, separated from origin of anal fin by 3 or 4 rows of scales and from end of anal fin by 2 or 3 rows of scales. Some 2 or 3 rows of scales between lateral line and first dorsal fin. Dorsal fin VI, 14 or 15. No evidence of elongation of any spine of the first dorsal fin. Predorsal length for first dorsal fin slightly shorter than head length. Pectoral fin relatively pointed at its outer edge with 19-22 branched rays. Anal fin with 15 or 16 rays. Caudal fin truncate, forming almost a

Table 4.5. Proportional measurements of Bembrops curvatura (n = 21) (expressed as thousandths of standard length).

CHARACTERS	HOLOTYPE	MEAN (RANGE)	SD
HDL	391	388.7 (362-429)	15.9
HDW	149	148.0 (132-161)	8.1
HDH	108	105.0 (97-120)	5.3
EYD	81	84.2 (72-102)	7.7
SNL	128	128.3 (119-137)	5.0
POL	190	181.2 (161-200)	9.6
TNTL	27	33.9 (23-48)	6.8
UPJL	142	143.5 (132-152)	5.7
BDD	114	121.9 (108-138)	9.1
PRDR1	385	374.4 (357-397)	12.8
PRDR2	558	546.7 (531-560)	9.6
PSDR1	520	533.8 (503-557)	15.9
PSDR2	117	128.6 (111-142)	7.9
PECFL	190	201.0 (184-229)	11.9
INPECD	124	119.9 (77-149)	15.4
PELFL	165	169.9 (157-183)	7.4
INPELD	65	64.2 (58-72)	3.3
IOW	14	13.4 (9-23)	2.9
LCPD	98	108.4 (94-124)	9.1
HCPD	60	57.8 (52-69)	3.9
DRFNB1	113	109.7 (95-129)	8.9
DRFNB2	341	342.3 (313-366)	15.3
ANLFNB	364	364.2 (344-388)	13.4
ANSANL	35	40.8 (26-55)	6.9

straight line at posterior edge. Gill rakers 3-5 on upper limb of branchial arch and 10-13 on lower limb.

Color in alcohol.-

Yellowish brown dorsally, posterior part of head between eyes darkest; light brown ventrally. Scales between dorsal fins and lateral line with dark brown edge. Series of 4-7 circular or oval dark brown spots below lateral line. Membranes between first two or three spines of first dorsal fin dark gray or black. Caudal fin with a dark (almost black in freshly preserved specimens) blotch near dorsal margin. Peritoneum light yellowish brown with a few spots in some specimens.

Remarks.-

PCA, which included all four species, shows that B. curvatura closely resembles B. caudimacula, B. magnisquamis and B. nematopterus in morphology (Fig. 4.3). The specimens of B. curvatura are distinctly separated from B. caudimacula, B. magnisquamis and B. nematopterus. See description of B. caudimacula for further details.

Distribution.-

Known from the Indo-West Pacific, from off Japan and surrounding areas, and from off Indonesia, and northwestern Australia (Fig. 4.12).

Biological Notes.-

All specimens for which depth information is available have been captured in the 100-280 m range. I have examined one female with mature ova collected in April off the coast of Japan.

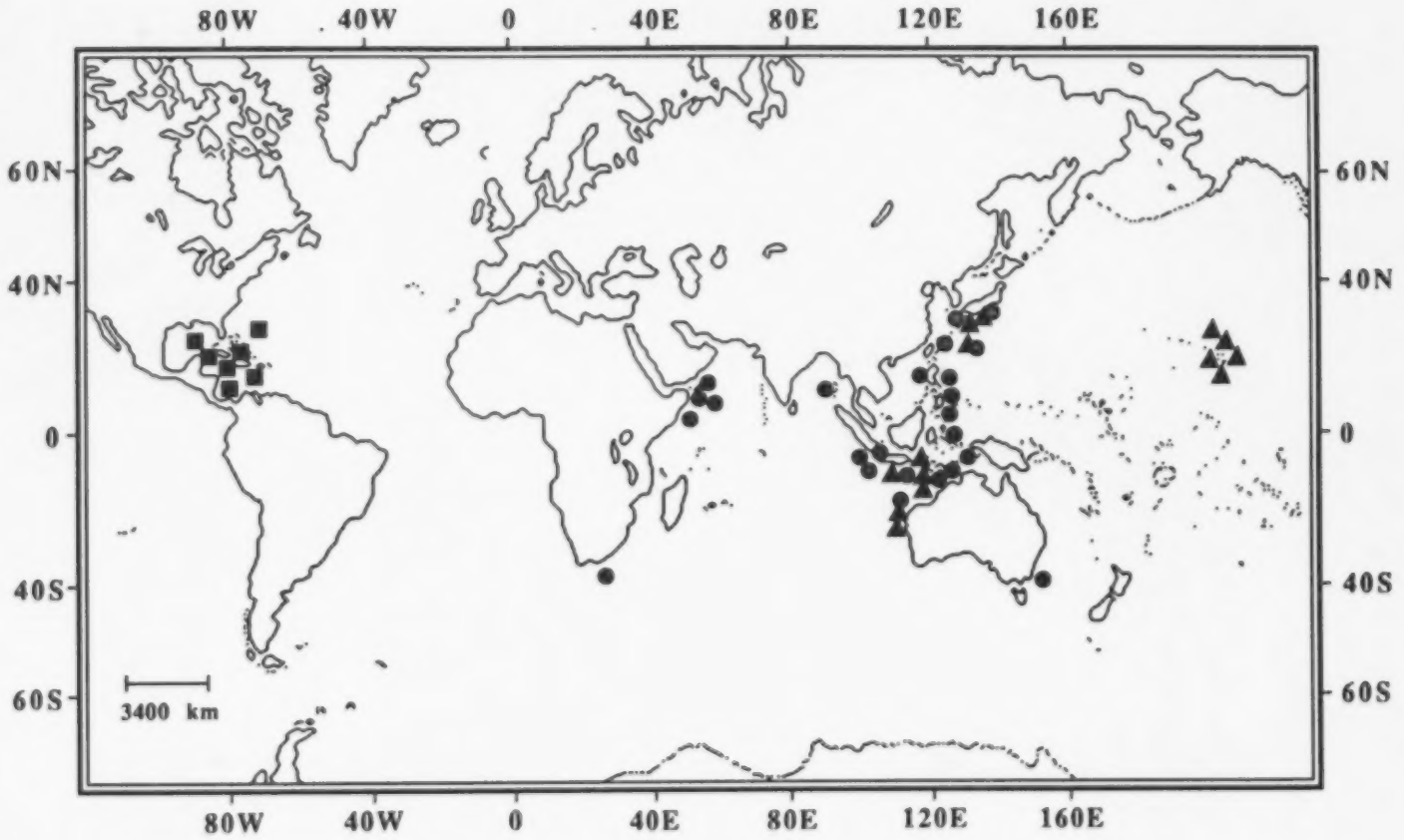


Fig.4.12. Geographic distribution of B. curvatura (●), B. filifera (▲), B. macromma (■), and B. platyrhynchus (●) based on data collected from original species descriptions, other literature sources, and museum collections.

Etymology.-

The specific name comes from the Latin word curvatura, meaning curvature, and refers to the sharply curved lateral line.

Materials Examined.- (21 specimens, 91.9 – 153.2 mm in SL).

FRLM 9768, 1: 133.3 mm SL (holotype), Owase, Mie Prefecture, Japan; BSKU uncat., 7: 137.8-153.2 mm SL, Tosa Bay, Japan; FRLM 9779-9786, 8: 91.9-135.6 mm SL, off Owashi, Pacific coast of Mie Prefecture, Japan. NTM S.10740-004, 1: 92.8 mm SL, southern Lombok, Indonesia; NTM S.10751-008, 1: 105.7 mm SL, Saleh Bay, Sumbawa, Indonesia; USNM 59647, 3: 91.2-104.8 mm SL, Kagoshima, Japan.

Bembrops filifera Gilbert, 1905

Bembrops filifera Gilbert, 1905: 643 (off northeast coast of Maui, Hawaii).

Bembrops filodorsalia Okada and Suzuki, 1952: 70 (Owashi, Mie Prefecture, Japan).

Bembrops indica McKay, 1971: 43 (Indian Ocean, off northern coast of Western Australia, Australia).

Bembrops filodorsalis (Okamura, Amaoka and Mitani, 1982: 386, erroneous spelling).

Diagnosis.-

L.L.scales 60-69; D.VI, 14-16; P.22-25; V.I, 5; A.16-18; C.11.

A relatively large species of Bembrops with gradually descending lateral line and small scales. Differs from B. anatirostris in having more anteriorly inserted dorsal fins, elongated first (instead of second or third) spine of first dorsal fin and fewer anal fin rays. Distinguished from B. gobioides in counts of lateral-line scales and second dorsal fin rays.

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.6.

Snout long with scales on dorsal and lateral sides. Upper jaw extending behind anterior margin of eye but not reaching its mid-line. Maxillary tentacle long and slender. Lateral line descending gradually in area of pectoral fin with 60-69 (only one specimen has 69 scales, others range from 60-66), separated from origin of first dorsal fin by 3-5, from origin of anal fin by 5-7 and from end of anal fin by 3 or 4 rows of scales. Dorsal fin VI, 14-16. Many adult specimens of both sexes with elongated first spine of first dorsal fin. Pectoral fin almost rounded with middle rays longest with 22-25 branched rays. Anal fin

Table 4.6. Proportional measurements of Bembrops filifera (n = 35) (expressed as thousandths of standard length).

CHARACTERS	HOLOTYPE	MEAN (RANGE)	SD
HDL	387	408.7 (357-486)	20.3
HDW	141	143.8 (126-166)	8.3
HDH	91	96.9 (85-115)	6.9
EYD	81	85.7 (74-104)	6.5
SNL	141	145.5 (128-180)	8.3
POL	171	181.4 (165-212)	8.2
TNTL	37	31.5 (20-43)	5.5
UPJL	148	152.4 (140-278)	6.6
BDD	118	111.0 (91-138)	12.6
PRDR1	386	404.2 (375-485)	17.9
PRDR2	551	568.3 (530-681)	25.3
PSDR1	520	515.4 (490-578)	16.9
PSDR2	122	110.6 (95-137)	7.4
PECFL	200	201.8 (185-244)	10.8
INPECD	127	121.4 (99-141)	10.4
PELFL	159	158.8 (143-185)	8.5
INPELD	73	74.8 (61-89)	7.1
IOW	12	12.3 (9-16)	1.6
LCPD	96	87.7 (74-108)	7.7
HCPD	50	49.9 (45-57)	2.9
DRFNB1	110	100.4 (74-122)	10.6
DRFNB2	352	341.3 (267-398)	19.7
ANLFNB	375	357.9 325-415)	19.7
ANSANL	42	39.5 (25-50)	5.9

with 16-18 rays. Caudal fin truncate. Gill rakers 3-6 on upper limb and 11-15 on lower limb of branchial arch.

Color in Alcohol.-

Yellowish brown to light yellowish dorsally, lighter ventrally. Tinker (1978) gave the body color as olive brown. Scales with darker edge. A series of 9-13 dusky spots along lateral line. Membranes between first three spines of first dorsal fin dark gray. Spot on dorsal edge of caudal fin distinct in some, inconspicuous in others. Peritoneum black to dark grayish in color.

Remarks.-

A close morphological similarity of this species to B. anatirostris was reported by Ginsburg (1955) and to B. gobioides by Grey (1959). PCA's using the combined data set, the truss data set, and the meristic data set separately were performed including these three species. A closer morphological similarity was observed between B. filifera and B. gobioides (Fig. 4.8) than with B. filifera and B. anatirostris. See accounts of B. anatirostris and B. gobioides for more details.

Nomenclatural Discussion.-

Gilbert (1905) based his description of B. filifera on a 223 mm long (in total length) male from the northeastern coast of Maui, Hawaiian Islands taken at a depth between 326 and 370 m. He also reported another immature specimen (53 mm long) from the same locality.

Okada and Suzuki (1952) described B. filodorsalia from a single female specimen collected from Owashi Fish Market, Mie Prefecture, Japan. Okada and Suzuki (1952) compared their holotype with descriptions of B. caudimacula, B. gobioides and B.

platyrhynchus to reach the decision that they had an undescribed species. However, they were probably unaware of the existence of B. filifera. The holotype of B. filodorsalia is presumed lost (S. Kimura, Mie University, pers. comm.). I consider this species a junior synonym of B. filifera based on my study of the original description and examination of three specimens collected at or near type locality. Okamura, Amaoka and Mitani (1982), in their book on fishes of the Kyushu-Palau Ridge and Tosa Bay, erroneously spelled the name B. filodorsalis.

Bembrops indica was described by McKay (1971) from a collection of fishes trawled off the northern coast of Western Australia. The holotype and four paratypes were collected at a depth of 350-370 m. Two other paratypes were collected at a shallower depth (62 m). McKay distinguished these specimens from B. filifera and designated them as a new species based on the following differences: anal fin rays 17 instead of 18, snout shorter, and coloration different. I have examined the holotype and one paratype, and in my opinion, separate species status for these specimens is unwarranted because their characters fall well within the range for B. filifera.

Distribution.-

Known from eastern Indian Ocean and western Pacific Ocean, from the coasts of Japan, Indonesia, Western Australia, and the Hawaiian islands (Fig. 4.12).

Biological Notes.-

The species occurs at a wide range of depths (from 62 to about 375 m) but mostly at depths over 300 m. I have examined female specimens with ripe eggs collected during February and March off the coast of Japan and during November from Hawaiian Islands.

Etymology.-

The species name is attributed to the filamentous nature of the elongated first spine of the first dorsal fin.

Materials Examined.- (35 specimens, 88.6-219.0 mm in SL).

USNM 051613, 1: 219.0 mm SL (holotype), northeastern coast of Maui, Hawaii; AMS I.21804-014, 1: 165.0 mm SL, North West Shelf, west of Darwin, Timor Sea, Australia; BSKU 12373, 1: 189.5 mm SL, Tosa Bay, Japan; BSKU 35489, 1: 193.5 mm SL, Tosa Bay, Japan; BSKU 35551-35553, 3: 180.0-197.0 mm SL, Tosa Bay, Japan; ex-BPBM 24273, 4: 162.2-206.5 mm SL, northwestern Maui, Hawaii (21°04'N, 156°31'W); ex-BPBM 24287, 20: 88.6-198.2 mm SL, northwestern Maui, Hawaii (21°04'N, 156°32'W); FRLM 9788, 1: 102.0 mm SL, off Owase, Pacific coast of Mie Prefecture, Japan; NTM S.11116-001, 1: 209.0 mm SL, south Java, Indonesia; NTM S.12001-004, 1: 148.5 mm SL, Roti area, Indonesia; WAM P.19138, 1: 163.0 mm SL (holotype of B. indica), Timor Sea, off the coast of Western Australia, Australia (17°17'S, 119°57'E); WAM P.19163, 1: 173.1 mm SL (paratype of B. indica), Timor Sea, off the coast of Western Australia, Australia (13°28'30"S' 123°09'10"E).

Other Materials Examined.-

USNM uncat., 22, Hawaiian Islands (21°N, 159°W); WAM P29729-016, 3, approx. 60 km west of Dowe Island, Western Australia, Australia (25°02'S, 112°09'E); WAM P29730-007, 3, approx. 60 km west of Dowe Island, Western Australia, Australia (25°02'S, 112°09'E).

Bembrops gobioides (Goode, 1880)

Hypsicometes gobioides Goode, 1880: 348 (off Long Island, New York, USA); Goode and Bean, 1896: 290; Jordan and Evermann, 1896: 2294.

Bembrops gobioides Ginsburg, 1955: 637.

Diagnosis.-

L.L.scales 60-66; D.VI, 16-17; P.22-26; V.I, 5; A.17-18; C.11.

A relatively medium-sized species of Bembrops characterized by high number lateral-line scales, short and stumpy maxillary tentacle, dark gray membrane between first and second spines of first dorsal fin, and lateral line descending abruptly beyond origin of pectoral fin. A member of the anatirostris species group (also including caudimaculata and heterurus) characterized by the extended anterior end of the third hypobranchial. Distinguished from B. anatirostris and B. filifera in number of second dorsal fin rays (16 or 17 in gobioides vs. 14 or 15 in anatirostris and 14-16 in filifera). Distinguished from B. curvatura in counts of lateral-line scales (40-49 in B. curvatura), second dorsal fin rays (14-15 in B. curvatura), and anal fin rays (15-16 in B. curvatura).

Description.-

Frequency distributions for nine meristics and proportions of measurements of 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.7.

Snout relatively short. Scales present on lateral and dorsal surfaces of snout. Upper jaw extending behind anterior margin of eye. Maxillary tentacle short and stumpy. Lateral line descending relatively abruptly beyond origin of pectoral fin with 60-66 scales, separated from origin of first dorsal fin by 4-6 rows of scales, from origin of anal fin by 5 or 6 rows of scales and from end of anal fin by 3 rows of scales. Dorsal fin VI, 16 or 17.

Table 4.7. Proportional measurements of Bembrops gobioides (n = 22) (expressed as thousandths of standard length). No holotype data due to poor condition of the type specimen.

CHARACTERS	MEAN (RANGE)	SD
HDL	353.1 (338-380)	13.2
HDW	132.1 (115-146)	8.7
HDH	96.2 (87-107)	7.1
EYD	93.3 (86-102)	5.4
SNL	113.1 (102-123)	5.6
POL	154.6 (142-169)	7.1
TNTL	24.7 (15-32)	4.3
UPJL	134.4 (126-146)	6.1
BDD	114.7 (87-146)	13.1
PRDR1	357.9 (340-380)	12.6
PRDR2	503.7 (479-526)	13.3
PSDR1	556.8 (528-577)	15.7
PSDR2	126.1 (115-140)	6.1
PECFL	237.5 (219-263)	11.4
INPECD	109.1 (94-120)	6.5
PELFL	147.5 (140-160)	6.3
INPELD	56.7 (49-64)	4.5
IOW	9.7 (7-14)	2.1
LCPD	111.5 (100-119)	6.1
HCPD	44.3 (34-49)	3.1
DRFNB1	100.1 (92-106)	3.3
DRFNB2	388.7 (351-412)	15.3
ANLFNB	403.1 (363-418)	13.7
ANSANL	37.5 (31-48)	4.3

No evidence of prolongation of any spine of first dorsal fin. Predorsal length for first dorsal fin almost equal to head length. Pectoral fin with 22-26 rays, broad at its base. Anal fin with 17 or 18 rays. Caudal fin rounded. Gill rakers 5 or 6 on upper limb and 12-14 on lower limb of branchial arch.

Color in Alcohol.-

Darker gray dorsally, lighter ventrally. Larger specimens generally darker than smaller ones. Scales with dark posterior edge. A series of 2 or 3 circular dark brown spots along lateral line in some specimens. Membrane between first and second spines of first dorsal fin dark gray; color restricted to upper edge in three specimens. Caudal fin with a prominent, large dark spot (circular, oval or elongated) on its dorsal edge. Peritoneum dark gray to black.

Remarks.-

Ginsburg (1955) mentioned a close similarity of this species to B. anatirostris and Grey (1959) compared it with B. macromma. The species shows distinct differences from B. macromma in the number of the second dorsal fin rays, the slope of the lateral line, and the presence of scales in the area in front of eye. It is also similar to B. filifera. The results of PCA using B. anatirostris, B. gobioides and B. filifera specimens was discussed in the description of B. anatirostris.

Nomenclatural Discussion.-

Goode (1880) erected the genus Hypsicometes for his new species, H. gobioides, which he described from an immature specimen (43.5 mm SL) collected from Long Island area, New York. Ginsburg (1955) considered the genus to be a junior synonym of Bembrops Steindachner, 1876. I have examined the holotype but was unable to use it in

any of my analyses because of its very poor condition. The holotype is from the northernmost locality for the genus and is the only specimen collected so far from the area. Although it would be desirable to examine a well-preserved specimen from the type locality to be certain of the identification, many examples collected from the Gulf of Mexico do confirm distinct species status of this species.

Distribution.-

Known from the western Atlantic, predominantly from the Gulf of Mexico (Fig. 4.9).

Biological Notes.-

Known to occur at depths of about 100 m to over 700 m, most prevalent in depths greater than 300 m. Staiger (1970), while studying the distribution of fishes in the Straits of Florida, found the species throughout the Straits at depths between 315 to 724 m.

Etymology.-

The specific name is in reference to the morphological similarity of the species to species of Gobius.

Materials Examined.- (22 specimens, 43.5 – 202.0 mm in SL).

USNM 26007, 1: 43.5 mm SL (holotype), off Long Island, New York (40°02'54"N, 70°23'40"W); GCRL 15095, 2: 151.4-153.0 mm SL, Gulf of Mexico; UF 12906, 10: 147.8-200.5 mm SL, Atlantic Ocean (29°04'N, 80°00'W); UF 13221, 9: 121.0-195.3 mm SL, Atlantic Ocean (29°04'N, 80°00'W).

Other Materials Examined.-

ISH 3591/79, 1, off Florida (29°07'N, 79°59'W); GCRL 15120, 2, Gulf of Mexico (29°10'N, 85°55'W); UF 40089, 10, Gulf of Mexico (27°45'N, 95°07'W); UF 40161, 6, Gulf of Mexico (27°25'N, 95°56'W); USNM 304917, 2, Caribbean Lesser Antilles (15°39'N, 61°10'W); USNM 304920, 2, Gulf of Mexico (28°33'N, 86°09'W).

Bembrops greyi Poll, 1959

Bembrops greyi Poll, 1959: 40 (39 miles north of Port Gentil, Gabon).

Diagnosis.-

L.L.scales 48-55; D.VI, 15-17; P.25; V.I, 5; A.18; C.11.

A medium-sized species of the genus characterized by dark brown to black pigmentation entirely or in most part on membranes of first dorsal fin.

Descriptions.-

Frequency distributions for nine meristics and proportions of measurements of 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.8.

Snout short. Scales on lateral and dorsal sides of snout. Upper jaw extending behind anterior margin of eye reaching almost to its mid-line. Lateral line descending adjacent to pectoral fin with 48-55 scales (three specimens I have examined have 52 and 55 scales), separated from origin of first dorsal fin by 2 or 3, from origin of anal fin by 5, and from end of anal fin by 3 rows of scales. Dorsal fin VI, 15-17 (three specimens used in this study have 16 and 17 rays). None of the spines of first dorsal fin prolonged. Predorsal length for first dorsal fin slightly less than head length. Pectoral fin almost rounded at its outer margin with 24-27 (three specimens in my study have 24 or 25) branched rays. Anal fin with 17 or 18 rays . Caudal fin almost rounded. Gill rakers, 5 on upper limb of branchial arch and 11 or 12 on lower limb in three specimens.

Table 4.8. Proportional measurements of Bembrops greyi (n = 3) (expressed as thousandths of standard length).

CHARACTERS	PARATYPE	MEAN (RANGE)	SD
HDL	390	401.0 (390-412)	15.5
HDW	142	151.5 (142-161)	13.4
HDH	109	109.0	0
EYD	104	107.0 (104-110)	4.2
SNL	115	119.0 (115-123)	5.6
POL	178	179.5 (178-181)	2.1
TNTL	34	32.0 (30-34)	2.8
UPJL	147	152.5 (147-158)	7.8
BDD	124	118.0 (112-124)	8.5
PRDR1	386	395.5 (386-405)	13.4
PRDR2	536	543.0 (536-550)	9.9
PSDR1	523	523.0	0
PSDR2	120	117.5 (115-120)	3.5
PECFL	229	230.5 (229-232)	2.1
INPECD	85	102.0 (85-119)	24.0
PELFL	148	153.0 (148-158)	7.1
INPELD	48	52.0 (48-56)	5.6
IOW	8	8.0	0
LCPD	110	105.5 (101-110)	6.4
HCPD	50	51.0 (50-52)	1.4
DRFNB1	95	99.0 (95-103)	5.6
DRFNB2	352	356.5 (352-361)	6.4
ANLFNB	376	378.0 (376-380)	2.8
ANSANL	34	35.5 (34-37)	2.1

Color in Alcohol.-

Light yellow dorsally, even lighter ventrally. Posterior edge of scales above lateral line dark brown to black. Membranes between all six spines of first dorsal fin entirely or in most part dark brown to black. Membranes between soft rays of second dorsal fin with scattered black spots. Base of pectoral fin dark brown. Prominent dark blotch on dorsal edge of caudal fin. Peritoneum almost black.

Remarks.-

Bembrops greyi can be distinguished from all other species by its dark first dorsal fin. However, it shows some similarity with B. platyrhynchus. PCA's were performed on the data sets comprising specimens of these two species. Scatter plots (Fig. 4.13) show that the two species can be separated on PCII of the combined data set and on the meristic PCI. Both data sets have heaviest loadings on the number of second dorsal and anal fin rays.

Distribution.-

Eastern Atlantic off coasts of Guinea, Gabon, Congo and Angola (Fig. 4.7).

Biological Notes.-

Known to occur on soft bottoms of the continental shelf at depths between 250 and 420 m. One female with matured ova collected in March. Feeds on other fish (Knapp, 1981).

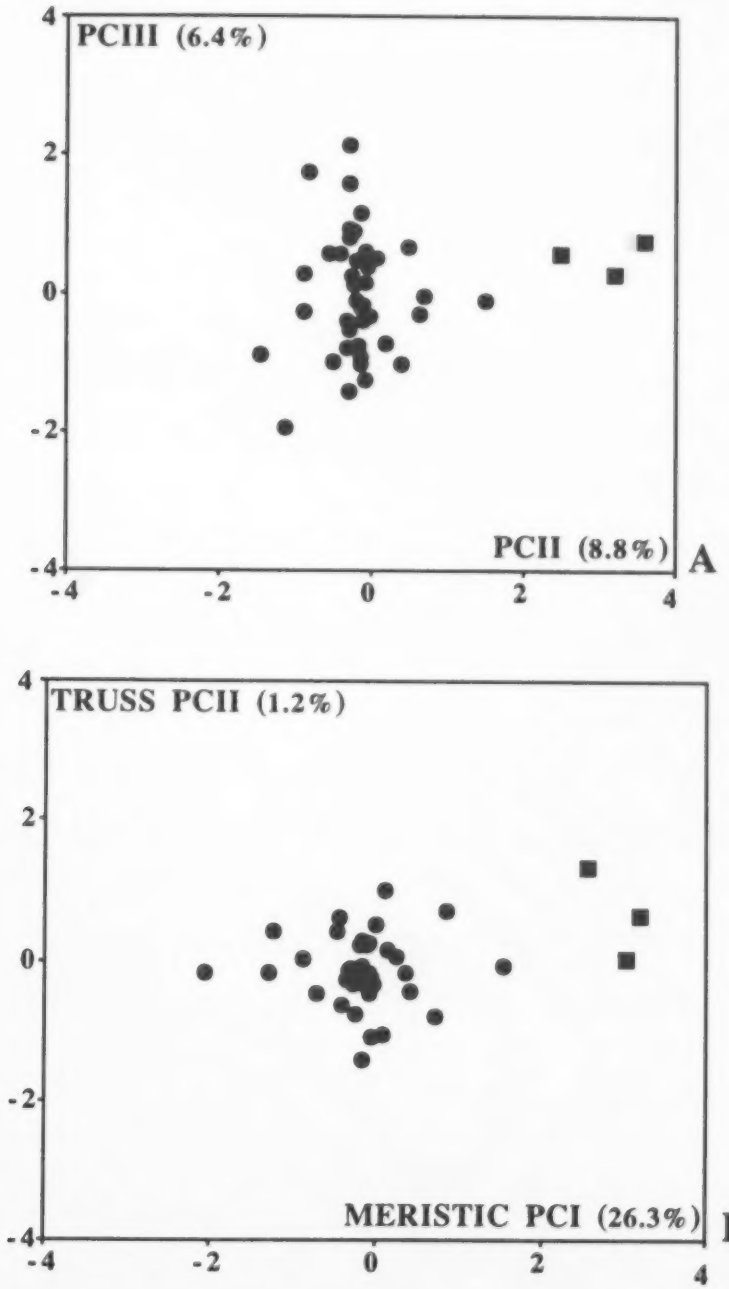


Fig. 4.13. PCA of B. greyi (■) and B. platyrhynchus (●). A. Scatter plot of PCII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data. Variance explained by each factor is given in parentheses.

Etymology.-

The species was named for Marion Grey who kindly provided necessary literature on Bembrops and also examined the type specimen to reconfirm the species status (Poll, 1959).

Materials Examined.- (3 specimens, 144.6 – 173.0 mm in SL).

ISNB 364, 1: 144.6 mm SL (paratype), Angola (10°05'S, 17°0'W); ISNB 13.695, 1: 163.5 mm SL, approx. 45 miles from Port Gentil, Gabon (00°40'S, 08°58'E); ISH 1223/64, 1: 173.0 mm SL, off coast of Guinea (09°58'N, 16°50'W).

Bembrops heterurus (Ribeiro, 1915)

Hypsicometes heterurus Ribeiro, 1915: 4 (coast off Rio de Janeiro, Brazil).

Bembrops heterurus Poll, 1959: 38 (Gulf of Guinea).

Diagnosis.-

L.L.scales 54-60; D.VI, 14-15; P.17-24; V.I, 5; A.16-18; C.11.

A species of Bembrops characterized by upper lobe of caudal fin elongated in an acute angle. A member of the anatirostris species group (also including caudimaculata and gobioides) defined by the extended anterior end of the third hypobranchial. Distinguished from B. caudimaculata and B. macromma in number of anal fin rays (17 in 84% of specimens vs. 18 in B. caudimaculata and 77% of B. macromma specimens).

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.9.

Snout short. Scales on lateral and dorsal surfaces of snout including area in front of eye. Upper jaw extending behind anterior margin of eye but not reaching its mid-line. Maxillary tentacle short. Lateral line descending gradually along dorsal edge of pectoral fin with 54-60 scales, separated from origin of first dorsal fin by 4 or 5 rows of scales, from origin of anal fin by 6 or 7 rows of scales and from end of anal fin by 3-5 rows of scales. Dorsal fin VI, 14 or 15. Pectoral fin somewhat rounded at its outer edge with 17-24 branched rays. Anal fin with 16-18 rays. Rays of upper lobe of caudal fin relatively elongated in undamaged specimens forming a somewhat acute angle with lower lobe; lower lobe truncate or rounded. Gill rakers 4-6 on upper limb and 12-15 on lower limb of branchial arch.

Table 4.9. Proportional measurements of Bembrops heterurus (n = 19) (expressed as thousandths of standard length). Holotype could not be located.

CHARACTERS	MEAN (RANGE)	SD
HDL	378.6 (361-406)	10.9
HDW	145.6 (133-170)	10.6
HDH	112.4 (101-128)	7.8
EYD	92.0 (83-110)	6.7
SNL	122.4 (112-132)	6.2
POL	170.0 (161-182)	6.1
TNTL	22.7 (13-33)	5.6
UPJL	146.2 (136-161)	6.5
BDD	133.3 (113-159)	12.2
PRDR1	386.0 (372-410)	9.6
PRDR2	547.6 (523-568)	11.3
PSDR1	533.8 (513-559)	10.5
PSDR2	131.2 (119-145)	7.6
PECFL	245.2 (234-259)	7.3
INPECD	126.5 (103-149)	13.3
PELFL	169.4 (161-182)	6.7
INPELD	69.6 (53-80)	6.4
IOW	11.0 (9-13)	1.0
LCPD	112.2 (99-124)	6.9
HCPD	47.9 (44-54)	2.7
DRFNB1	106.5 (77-119)	9.5
DRFNB2	342.4 (326-365)	9.4
ANLFNB	372.5 (358-390)	7.4
ANSANL	30.3 (25-37)	3.6

Color in Alcohol.-

Light yellowish to yellowish brown dorsally, light yellowish brown to creamy – brown ventrally. A series of six to eight oval-shaped dusky spots along lateral line. Membrane between first and second spines of first dorsal fin dark gray. Peritoneum dark gray to black.

Remarks.-

B. heterurus was compared with B. caudimaculata, B. macromma, and B. morelandi using two combinations of species (one combination includes specimens of B. caudimaculata, B. macromma and B. heterurus, whereas the other includes B. morelandi instead of B. caudimaculata). Principal components scores were computed using the combined data set and the truss and meristic data set for both combinations. See B. caudimaculata account for more details on the first combination. In both scatter plots (Fig. 4.14) of the second combination of species, the single specimen of B. morelandi shows closer similarity with the specimens of B. heterurus. B. heterurus is separated on the PCII axis from the other three species by a contrast among the number of scale rows between the lateral and the origin of the first dorsal fin. The slope of the lateral line, and the number of anal fin rays in the combined data set, and the number of scales between the first dorsal fin spine and the lateral line and the anal fin ray number, have the highest loadings among the meristic characters.

I was unable to locate the type specimen of B. heterurus owing to lack of information in the original description. However, most of the specimens used in this study came from the type locality or its vicinity.

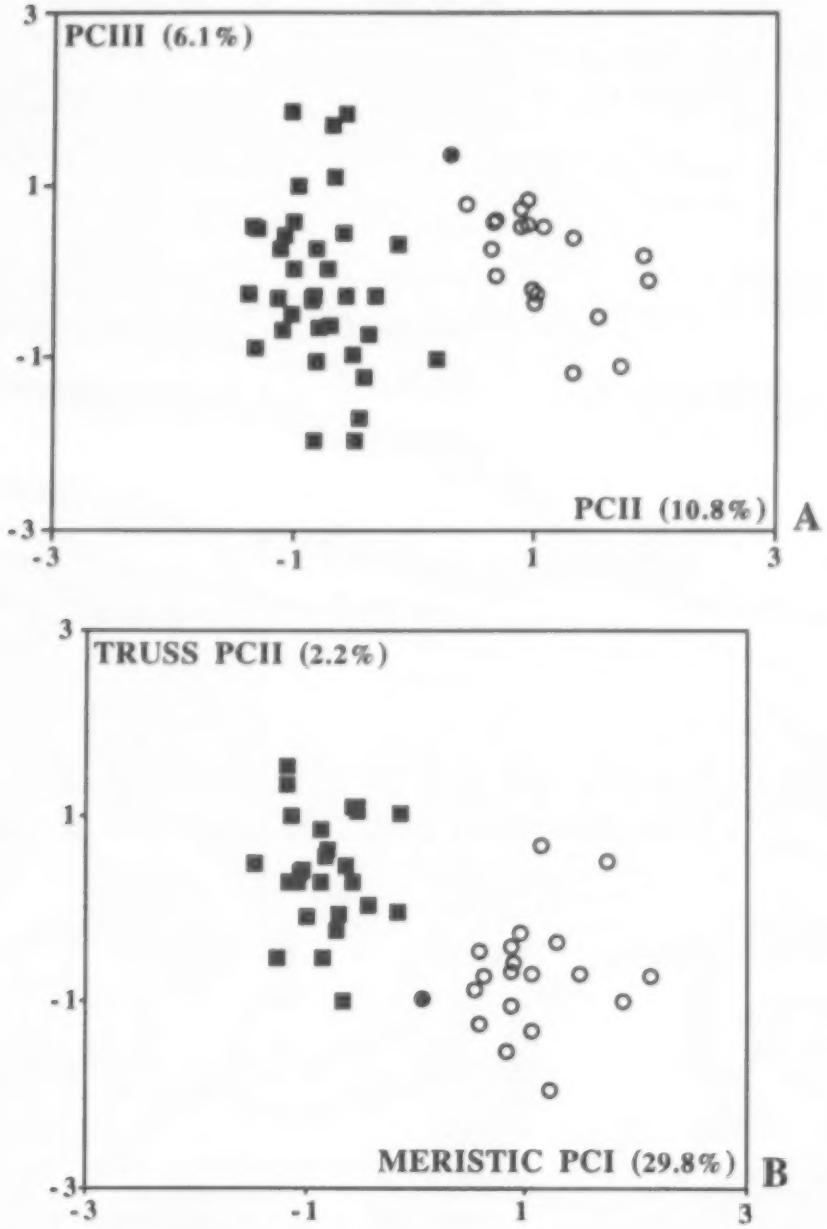


Fig. 4.14. PCA of B. heterurus (o), B. macromma (■) and B. morelandi (●). A. Scatter plot of PCII of combined truss, meristic and attribute data. B. Scatter plot of PCI of meristic and attribute data and PCII of truss data. Variance explained by each factor is given in parentheses.

Nomenclatural Discussion.-

Poll (1959) identified a number of specimens from the Gulf of Guinea off the coast of Africa as B. heterurus and considered that species a senior synonym of B. caudimaculata. My examination of the holotype of B. caudimaculata suggests that the two species are not conspecific.

Distribution.-

Atlantic. Known from off the coast of Brazil in the western Atlantic and the Gulf of Guinea in the eastern Atlantic (Fig. 4.9).

Biological Notes.-

Occurs at depths between 100 and 390 m (Poll, 1959). All specimens I have studied came from relatively shallow water at depths between about 90 to 200 m. Females with mature ova were collected in August from the Gulf of Guinea (Poll, 1959). Principle prey items are crustaceans and other fishes (Poll, 1959; Knapp, 1981).

Etymology.-

Not specified in the original description, but the specific name is from the Greek heteros, meaning different, and oura meaning tail.

Materials Examined.- (19 specimens, 82.5 – 160.0 mm in SL).

FURG uncat., 4: 117.5-160.0 mm SL, Rio Grande do Sul, Brazil; FURG uncat., 5: 114.7-128.1 mm SL, Rio Grande do Sul, Brazil; FURG uncat., 5: 90.0-115.1 mm SL, Rio Grande do Sul, Brazil; MZUSP 38917, 2: 82.5-120.5 mm SL, off Brazil (23°15'S,

42°24'W); MZUSP 38918, 2: 130.7-135.2 mm SL, off Brazil (30°28'S, 48°42'W); UAMZ 4647, 1: 122.3 mm SL, Rio Grande do Sul, Brazil (32°41'S, 50°35'W).

Other Materials Examined.-

IRSNB 13.679, 3, off Liberia (05°52'S, 11°43'E); IRSNB 13.687, 10, off Gabon (00°45'S, 08°58'E); ISH 1144/64, 1, off coast of Liberia (06°32'N, 11°29'W); ISH 1271/64, 2, off coast of Ivory Coast (05°12'N, 04°09'W); MZUSP 38919, 4 (30°40'S, 49°09'W); UF 47051, 1, off Gabon (00°02'S, 08°02'E); USNM 304919, 26, Guinea (09°43'N, 16°08'W).

Bembrops macromma Ginsburg, 1955

Bembrops macromma Ginsburg, 1955: 634 (off Virgin Islands).

Diagnosis.-

L.L.scales 54-64; D.VI, 14-15; P.22-24; V.I, 5; A.17-18; C.11.

A medium-sized species of Bembrops characterized by truncated caudal fin with dark gray pigmentation along its entire posterior edge and absence of scales in a small area in front of eye. Further distinguished from B. caudimaculata by its larger eye and from B. heterurus by its relatively gradual slope of lateral line, which can be further demonstrated by the number of scale rows between lateral line and origin of first dorsal fin ($\overline{X}$ = 3.3 in macromma vs. $\overline{X}$ = 4.9 in heterurus). Differentiated from B. morelandi in having relatively lighter peritoneum.

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.10.

Snout relatively short. Scales on lateral and dorsal sides of snout in most specimens (approximately 92% of the specimens examined); a small area in front of eye without scales in most specimens. Upper jaw extending behind anterior margin of eye reaching almost to its mid-line. Maxillary tentacle short and stubby. Lateral line descending gradually, reaching mid-line at tip of pectoral fin with 54-64 scales, separated from origin of first dorsal fin by 3-5 rows of scales, from origin of anal fin by 5-7 rows of scales and from end of anal fin by 2 or 3 rows of scales. Dorsal fin VI, 14-15. Second spine of first dorsal fin prolonged in some specimens. Pectoral fin pointed at its outer edge in most specimens

Table 4.10. Proportional measurements of Bembrops macromma (n = 35) (expressed as thousandths of standard length).

CHARACTERS	HOLOTYPE	MEAN (RANGE)	SD
HDL	390	391.0 (367-433)	16.8
HDW	169	155.8 (134-177)	10.7
HDH	124	116.5 (97-131)	8.4
EYD	107	109.3 (93-137)	10.2
SNL	123	119.9 (108-149)	10.0
POL	167	174.6 (164-194)	8.0
TNTL	16	22.0 (12-41)	7.9
UPJL	146	146.8 (114-169)	10.0
BDD	130	120.0 (104-139)	8.8
PRDR1	380	385.3 (362-434)	17.8
PRDR2	555	555.7 (539-594)	12.4
PSDR1	532	523.6 (475-552)	17.8
PSDR2	142	134.8 (112-149)	9.3
PECFL	223	243.9 (223-265)	10.9
INPECD	128	123.2 (102-152)	11.1
PELFL	182	180.7 (161-204)	10.8
INPELD	68	64.0 (46-77)	6.2
IOW	11	9.4 (6-11)	1.4
LCPD	105	100.6 (76-118)	11.2
HCPD	51	51.8 (46-58)	3.4
DRFNB1	116	111.7 (89-137)	9.6
DRFNB2	331	327.3 (306-348)	10.8
ANLFNB	361	365.8 (333-395)	13.8
ANSANL	28	38.9 (28-57)	6.4

with 22-24 branched rays. Anal fin with 17 or 18 rays. Caudal fin truncate. Gill rakers 4-6 on upper limb of branchial arch and 12-15 on lower limb.

Color in Alcohol.-

Light to dark yellowish brown dorsally, relatively light ventrally. A series of three to nine large and small dusky spots along lateral line. Membranes between first, second, and third spines of first dorsal fin dark gray to black for entire height. Ginsburg (1955) observed "a small black spot at base of [first dorsal] fin behind third spine" in one specimen. Entire posterior edge of caudal fin dark gray to black in most specimens, lighter in others. Peritoneum dark gray to black.

Remarks.-

Bembrops macromma is morphologically similar to B. caudimaculata and B. heterurus. Results of the PCA (Fig. 4.11) show that B. macromma can be separated from the holotype of B. caudimaculata and the specimens of B. heterurus on PCII of the combined data set and also on meristic PCI. See B. caudimaculata account for more information on comparison.

Distribution.-

Known from the Gulf of Mexico and the Caribbean Sea (Fig. 4.12).

Biological Notes.-

Occurs at depths of about 150 to 550 m. Based on the depth information available from the specimens examined, the species is more common at depths below 250 m. Female specimens with mature gonad were collected in May.

Etymology.-

The specific name is derived from the Greek makros, meaning large, and omos, meaning shoulder.

Materials Examined.- (35 specimens, 78.8 – 232.2 mm in SL).

USNM 108392, 1: 153.7 mm SL (holotype), West Indies, Virgin Islands (18°35'30"N, 65°23'50"W); UF 15615, 2: 125.4-130.3 mm SL, southwest Caribbean off Nicaragua (16°08'N, 81°13'W); UF 47052, 2:102.1-113.2 mm SL, Caribbean Sea south of Jamaica (17°50'N, 77°52'W); USNM 304921, 2: 120.4-232.2 mm SL, Caribbean Sea off Colombia (11°09'N, 74°24'W); USNM 304922, 6: 100.7-153.6 mm SL, Puerto Rico (18°26'N, 67°11'30"W); USNM 304923, 8: 78.8-101.7 mm SL, Caribbean Sea off Jamaica (17°50'N, 77°52W); USNM 304925, 3: 98.8-144.2 mm SL, Great Bahama Bank area off Cuba (23°04'N, 78°46'W); USNM 304926, 4: 84.5-111.7 mm SL, Leeward Islands (17°38'30"N, 62°16'W); USNM 304927, 3: 125.0135.1 mm SL, Caribbean Sea near Antigua Island (17°27'N, 62°04'W); USNM 304928, 2: 94.1-102.5 mm SL, Off Jamaica (17°50'N, 77°52'W); USNM 304929, 2: 115.0-157.2 mm SL, Nicaragua (14°17'N, 81°55'W).

Bembrops magnisquamis Ginsburg, 1955

Bembrops magnisquamis Ginsburg, 1955: 633 (off Santiago, Cuba).

Diagnosis.-

L.L.scales 45-50; D.VI, 15-16; P.21-22; V.I, 5; A.17; C.11.

A small to medium-sized member of the genus with gradual slope of lateral line. Distinguished from B. caudimacula by higher number of fin rays in second dorsal fin and presence of dark brown pigmentation at base of membranes between anterior four spines of first dorsal fin.

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.11.

Snout relatively shorter with scales on lateral and dorsal surfaces including the area in front of eye. Upper jaw reaching behind anterior margin of eye. Maxillary tentacle long, tapering at the end. Lateral line sloping down gradually along pectoral fin with 45-50 scales, separated from origin of anal fin by 4-5 rows and from end of anal fin by 2 rows of scales. 2-4 rows of scales between lateral line and origin of first dorsal fin. Dorsal fin VI, 15-16. Spines of first dorsal fin not elongated. Pectoral fin with 21-22 branched rays. Anal fin with 17 rays. Caudal fin rounded. Gill rakers 4-5 on upper limb and 12-14 on lower limb of first branchial arch.

Table 4.11. Proportional measurements of Bembrops magnisquamis (n = 5) (expressed as thousandths of standard length).

CHARACTERS	HOLOTYPE	MEAN (RANGE)	SD
HDL	363	375.2 (357-399)	19.3
HDW	148	143.8 (135-152)	6.5
HDH	98	96.6 (92-99)	2.8
EYD	105	106.8 (101-116)	5.9
SNL	100	111.4 (100-119)	7.8
POL	151	169.6 (151-195)	17.5
TNTL	39	41.8 (32-52)	7.8
UPJL	140	143.8 (140-150)	4.5
BDD	96	96.2 (86-106)	7.1
PRDR1	379	373.0 (364-379)	6.7
PRDR2	537	536.2 (423-545)	8.1
PSDR1	553	550.6 (540-565)	9.4
PSDR2	139	128.4 (120-139)	7.8
PECFL	196	205.6 (196-225)	11.5
INPECD	134	117.2 (95-134)	14.0
PELFL	141	156.8 (141-177)	14.4
INPELD	76	68.2 (58-77)	8.2
IOW	11	11.0 (8-16)	3.1
LCPD	107	98.4 (88-107)	8.0
HCPD	58	55.2 (50-61)	4.4
DRFNB1	107	111.4 (102-123)	8.7
DRFNB2	352	357.8 (349-367)	7.6
ANLFNB	362	372.4 (362-380)	6.5
ANSANL	59	50.8 (46-59)	5.6

Color in Alcohol.-

Uniformly light yellowish brown. Membranes between first four spines of first dorsal fin are dark brown at their base. Anal fin with faint brown margin. Caudal fin with a light-brown transverse patch running along its dorsal edge in some specimens. Peritoneum light brown with occasional dark brown spots.

Remarks.-

Bembrops magnisquamis is morphologically very similar to B. caudimacula and B. nematopterus. Principal components analyses showed that in spite of the strong similarity, this species can be distinguished from others based on the differences in the length of the second dorsal fin, the number of fin rays in the second dorsal fin and the anal fin, and the number of scales between the last anal fin ray and the lateral line (Figs. 4.3 and 4.4). The morphometric analyses are discussed in detail in the description of B. caudimacula.

Distribution.-

Known from the Caribbean Sea (Fig. 4.7).

Biological Notes.-

A deeper-water species, occurring at depths between 350 and 465 m. Females with ripe ova collected in May.

Etymology.-

The specific name is derived from the Latin magnus, meaning large, and squama, meaning scale.

Materials Examined.- (5 specimens, 84.3 – 105.2 mm in SL).

USNM 045985, 1: 84.3 mm SL (holotype), Caribbean Sea off Santiago, Cuba (19°56'N, 75°47'30"W); USNM 304924, 4: 86.8-105.2 mm SL, Caribbean Sea off Costa Rica (12°31'N, 82°21'W).

Bembrops morelandi Nelson, 1978

Bembrops morelandi Nelson, 1978: 238 (northwestern part of Bay of Plenty, New Zealand).

Diagnosis.-

L.L.scales 56-58; D.VI, 13-14; P.25-26; V.I, 5; A.16-17; C.11.

A species of Bembrops with the following combination of characters: 56-58 lateral-line scales, about four large spots along lateral line, and jet-black peritoneum.

Description.-

Some nine meristic characters for the holotype and the paratype, and proportions for 24 morphometric characters for the paratype (expressed as thousandths of SL) are given in Tables 4.1 and 4.12.

Snout relatively long. Scales on lateral and dorsal sides of snout. Upper jaw reaching midway between anterior margin and middle of eye. Maxillary tentacle long and slender. Lateral line descending gradually in area of pectoral fin with 56 or 58 scales, separated from origin of first dorsal fin by 3 rows of scales, from origin of anal fin by 6 rows of scales and from end of anal fin by 3 rows of scales. Dorsal fin VI, 13 or 14. Nelson (1978) stated that the first spine of first dorsal fin shows some evidence of prolongation in larger specimen (not shown by the paratype I have examined). Pectoral fin rounded at its outer edge with 25 or 26 branched rays. Anal fin with 16 or 17 rays. Caudal fin rounded. Gill rakers 4 on upper limb and 15 on lower limb of branchial arch.

Table 4.12. Proportional measurements of Bembrops morelandi (n = 1) (expressed as thousandths of standard length).

CHARACTERS	PARATYPE
HDL	419
HDW	157
HDH	96
EYD	86
SNL	139
POL	190
TNTL	43
UPJL	162
BDD	111
PRDR1	407
PRDR2	574
PSDR1	514
PSDR2	144
PECFL	204
INPECD	123
PELFL	154
INPELD	80
IOW	13
LCPD	108
HCPD	54
DRFNB1	115
DRFNB2	314
ANLFNB	336
ANSANL	50

Color in Alcohol.-

Yellowish gray dorsally, slightly lighter ventrally. Scales with indistinct brown posterior edge. A series of four large dusky spots along lateral line. Entire membrane between first and second spines of first dorsal fin jet black; pigmentation extends along lower half of membranes between second and fourth spines. Black band along entire dorsal and basal edge of second dorsal fin. Caudal fin with two dark spots on its dorsal edge and a dark hollow circular spot in the middle (observed in the paratype). Peritoneum with jet-black pigmentation.

Remarks.-

Bembrops morelandi was compared with B. heterurus and B. macromma because of their morphological similarity. Scores for the second and third principal components for the combined data set, and the first PC for the meristic and the second PC for the truss data set were plotted as scatter plots (Fig. 4.14). See account of B. heterurus for a detailed discussion of the morphometric analysis.

My counts for the paratype generally agree with those of Nelson (1978). The morphometric measurements show slight differences.

Distribution.-

This species is known only from the holotype and paratype, which were collected from the northwestern part of the Bay of Plenty, New Zealand (Fig. 4.7).

Biological Notes.-

Both holotype and paratype were collected by trawling at depths between 366 and 395 m. Both specimens are adult males; the testes in the holotype are larger than those in the paratype (Nelson, 1978).

Etymology.-

B. morelandi is named for Dr. J. M. Moreland of National Museum of New Zealand, in recognition of his contribution to the study of fishes of New Zealand (Nelson, 1978).

Materials Examined.- (1 specimen, 207.0 mm in SL).

NMNZ P.7581, 1 (paratype), northwestern part of the Bay of Plenty, New Zealand (36°30'S, 176°10'E).

Bembrops nematopterus Norman, 1939

Bembrops nematopterus Norman, 1939: 70 (Zanzibar).

Diagnosis.-

L.L.scales 44-48; D.VI, 13-14; P.21-22; V.I, 5; A.16; C.11.

A smaller species than any other Bembrops, with gradually sloping lateral line, fewer lateral-line scales, fewer scale rows between lateral line and origin of first dorsal fin, and almost black pigmentation on membrane between anterior two spines of first dorsal fin.

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.13.

Snout moderately long. Scales on lateral and dorsal sides of snout including the area in front of eye. Upper jaw extending behind anterior margin of eye reaching almost to the mid-line. Maxillary tentacle long. Lateral line rising sharply above pectoral fin at base for 2-2.5 scale rows and then descending gradually along length of pectoral fin with 44-48 scales, separated from origin of first dorsal fin by 2 rows, from origin of anal fin by 5 rows and from end of anal fin by 3 rows of scales. Dorsal fin VI, 13-14. First spine of the first dorsal fin prolonged, even in a relatively young specimen. Predorsal length for first dorsal fin almost equal to head length. Pectoral fin longer than pelvic fin, rounded at its outer edge with 21-22 branched rays. Anal fin with 16 rays. Caudal fin rounded. Gill rakers 5 on upper limb of branchial arch and 15 or 16 on lower limb.

Table 4.13. Proportional measurements of Bembrops nematopterus (n = 3) (expressed as thousandths of standard length).

CHARACTERS	HOLOTYPE	MEAN (RANGE)	SD
HDL	400	401.3 (381-423)	21.0
HDW	159	160.6 (159-162)	1.5
HDH	116	118.0 (116-122)	3.5
EYD	102	101.0 (95-106)	5.6
SNL	134	131.7 (129-134)	2.5
POL	173	169.3 (161-174)	7.2
TNTL	18	28.7 (18-36)	9.4
UPJL	158	155.7 (146-163)	8.7
BDD	133	128.3 (123-133)	5.0
PRDR1	391	395.3 (386-409)	12.1
PRDR2	561	555.3 (542-563)	11.6
PSDR1	521	519.3 (508-529)	10.6
PSDR2	114	123.3 (114-138)	12.8
PECFL	209	213.0 (191-239)	24.2
INPECD	117	125.3 (117-131)	7.4
PELFL	155	163.0 (155-168)	7.0
INPELD	105	90.7 (72-105)	16.9
IOW	12	11.3 (11-12)	0.6
LCPD	96	99.7 (96-107)	6.3
HCPD	58	57.0 (55-58)	1.7
DRFNB1	109	103.7 (98-109)	5.5
DRFNB2	333	336.3 (333-341)	4.1
ANLFNB	345	349.0 (345-353)	4.0
ANSANL	29	34.3 (29-43)	7.6

Color in Alcohol.-

Yellowish brown dorsally and dorsolaterally, lighter below. Scales, especially on and close to dorsal side, with dark-brown edge. A series of 2-4 oval, brown, indistinct blotches along lateral line. Norman (1939) also noted some yellowish-green markings on head. Membrane between first two spines of first dorsal fin almost black distally. Membranes between rays of second dorsal fin with few brown spots. A thick, dark-brown line along ventral edge of caudal fin, and an indistinct brown blotch on dorsal edge. Peritoneum light brown with scattered dark spots.

Remarks.-

Bembrops nematopterus is morphologically similar to B. caudimacula and B. magnisquamis. Smith (1965) synonymized this species with B. caudimacula. The morphometric analyses revealed that B. nematopterus can be considered a valid species (Figs. 4.3 and 4.5). Prolongation of the first spine of the first dorsal fin, distance between end of second dorsal fin and end of anal fin, and number of scale rows between the lateral line and origin of first dorsal fin are some of the characters by which this species can be distinguished from the other two species. A detailed discussion of principal components analyses is given in the description of B. caudimacula.

Distribution.-

Known from the western Indian Ocean off the coast of Zanzibar, Africa (Fig. 4.7).

Biological Notes.-

Occurs at depths of 183 to 293 m (Norman, 1939).

Etymology.-

The specific name is derived from the Greek nematos, meaning thread, and pteros, meaning wing or fin, and refers to the thread-like elongation of the first spine of the first dorsal fin.

Materials Examined.- (3 specimens, 109.7 – 142.9 mm in SL).

BMNH 1939.5.24: 1272-7, 2: 137.0 mm SL (holotype), 142.9 mm SL (paratype), off Zanzibar; BMNH 1939.5.24: 1278-80, 1: 109.7 mm SL, off Zanzibar.

Bembrops platyrhynchus (Alcock, 1893)

Bathypercis platyrhynchus Alcock, 1893: 178 (Bay of Bengal, India).

Bembrops platyrhynchus Alcock, 1894: 118.

Bembrops filifer Fowler, 1938: 92 (Anima Sola Island, N., between Burias and Luzon, The Philippines).

Bembrops philippinus Fowler, 1939: 2.

Bembrops filamentosa Norman, 1939: 70.

Bembrops aethalea McKay, 1971: 42 (Indian Ocean, off northern coast of Western Australia, Australia).

Diagnosis.-

L.L.scales 47-57; D.VI, 13-16; P.22-25; V.I, 5; A.15-17; C.11.

A medium-sized species of the genus with gradually descending lateral line, relatively few lateral-line scales, and dark gray to black pigmentation on dorsal edge of membranes between all spines of first dorsal fin. Distinguished from B. caudimacula in having fewer scales between lateral line and origin of anal fin (4-6 in B. platyrhynchus vs. 5-7 in B. caudimacula). Further distinguished from B. greyi in having dark pigmentation only along dorsal edge of first dorsal fin.

Description.-

Frequency distributions for nine meristic characters and proportions for 24 morphometric characters (expressed as thousandths of SL) are given in Tables 4.1 and 4.14.

Table 4.14. Proportional measurements of Bembrops platyrhynchus (n = 43) (expressed as thousandths of standard length). Missing data is indicated by '?'.

CHARACTERS	HOLOTYPE	MEAN (RANGE)	SD
HDL	469	406.6 (382-469)	17.8
HDW	158	154.0 (136-181)	9.3
HDH	128	110.7 (91-133)	9.3
EYD	125	107.3 (88-135)	11.4
SNL	131	130.4 (113-160)	8.2
POL	237	178.3 (161-237)	13.1
TNTL	40	36.5 (18-82)	11.0
UPJL	171	153.6 (138-183)	8.5
BDD	128	127.8 (101-160)	12.3
PRDR1	438	408.0 (380-440)	15.8
PRDR2	591	567.6 (539-602)	15.6
PSDR1	486	508.3 (478-564)	18.7
PSDR2	116	125.5 (96-144)	9.6
PECFL	?	225.9 (167-255)	20.1
INPECD	116	120.4 (87-154)	13.4
PELFL	?	164.6 (147-183)	8.3
INPELD	64	64.0 (52-85)	8.7
IOW	12	9.9 (5-22)	4.2
LCPD	103	108.2 (97-132)	6.7
HCPD	56	60.7 (52-69)	3.9
DRFNB1	97	110.2 (90-129)	8.2
DRFNB2	331	327.8 (300-373)	14.2
ANLFNB	333	339.6 (313-398)	17.5
ANSANL	?	37.5 (26-53)	5.7

Snout moderately long with scales on lateral and dorsal sides. Upper jaw extending behind anterior margin of eye. Maxillary tentacle long and slender, somewhat pointed at its tip. Lateral line descending gradually along dorsal edge of pectoral fin with 47-57 scales, separated from origin of first dorsal fin by 2-4, from origin of anal fin by 4-6 and from end of anal fin by 3 or 4 rows of scales. Dorsal fin VI, 13-16. First spine of first dorsal fin elongated in some adult specimens. Predorsal length for first dorsal fin almost equal to head length. Pectoral fin moderately pointed at its posterior edge and with 22-25 branched rays. Anal fin with 15-17 rays. Caudal fin rounded. Gill rakers 3-5 on upper limb and 11-15 on lower limb of branchial arch.

Color in Alcohol.-

Yellowish brown dorsally, lighter ventrally with 8-13 large dark-brown spots along lateral line. Dorsal edge of membranes between all spines of first dorsal fin blackish dark gray to black. Dorsal and ventral edge of caudal fin with dark blotch; a dark caudal spot sometime present at upper base. Peritoneum dark grayish to pale black.

Remarks.-

Bembrops platyrhynchus has a strong phenetic similarity to B. caudimacula leading many workers (Alcock, 1899, 1902; Kuroda, 1950; Smith, 1965) to consider it to be a junior synonym of B. caudimacula. Morphometric analyses (Fig. 4.6) undertaken in this study also show a close resemblance between the two species. Presence of dark pigmentation on the membranes between all six spines of the first dorsal fin is a distinguishing character between the two species. A number of osteological characters also show differences, and are discussed in the section dealing with the phylogeny of the genus (Chapter 6). See also B. caudimacula account.

Bembrops platyrhynchus is also compared with B. greyi, and scatter plots of the three data sets (Fig. 4.13) show distinct separation of the two species.

Nomenclatorial Discussion.-

Alcock (1893) erected a new genus and species, Bathypercis platyrhynchus, to describe a 109 mm long specimen collected by the Indian Marine Survey Steamer 'Investigator' from the Bay of Bengal. At the time Alcock described this new species, he was unaware of the genus Bembrops Steindachner, 1876, which he acknowledged in a subsequent publication (Alcock, 1894) and considered Bathypercis as a junior synonym of Bembrops. As mentioned in the remarks section, B. platyrhynchus has been considered a junior synonym of B. caudimacula by many earlier workers. My detailed study of the two species suggests this synonymy to be unwarranted.

Fowler (1938) described B. filifer from several specimens collected in the Philippines Seas. Later Fowler (1939) renamed his species B. philippinus because of the close similarity of the specific name with B. filifera. Norman (1939) proposed B. filamentosa for B. filifer, citing preoccupation of the name. Norman suggested a close relationship of the species with B. caudimacula and also noted that B. philippinus differs from Alcock's figure in having a larger eye, a more posterior insertion of the first dorsal fin, and a notched edge of anal fin. My examination of the holotype and several paratypes of B. philippinus shows no distinct difference.

Bembrops aethalea was described by McKay (1971) from samples taken off the northern coast of Western Australia. My examination of the holotype and four paratypes of B. aethalea revealed that the species is conspecific with B. platyrhynchus.

Distribution.-

Known from the Indo-West Pacific, including the Bay of Bengal, the South China Sea, the Philippine Sea, the Tasman Sea, and off the coast of Somalia and South Africa (Fig. 4.12).

Biological Notes.-

Occurs at depths of about 100 to 350 m. One female specimen with mature ova was collected in the Philippine Sea in March.

Etymology.-

The specific name is derived from the Greek platys, meaning flat, and rhynchos, meaning snout or beak.

Materials Examined.- (43 specimens, 51.6-214.0 mm in SL).

ZSI 13437, 1: 88.5 mm SL (holotype), Bay of Bengal, India; WAM P.19144, 1: 178.8 mm SL (holotype of B. aethalea), Indian Ocean off northern coast of Western Australia, Australia (13°45'S, 123°30'50"E); WAM P.19148-19151, 4: 121.4-182.1 mm SL (paratypes of B. aethalea), Indian Ocean off northern coast of Western Australia, Australia (13°47'S, 123°18'E); USNM 098866, 1: 214.0 mm SL (holotype of Bembrops philippinus), east of Masbate Island, Anima Sola Island, N., the Philippines (12°52'N, 123°23'30"E); USNM 098940, 2: 141.4-194.6 mm SL (paratypes of B. philippinus), north of Tawi Tawi, the Philippines (05°28'30"N, 120°02'27"E); USNM 098944, 4: 109.3-196.2 mm SL (paratypes of B. philippinus), between Cebu and Bohol, the Philippines (10°08'50"N, 123°50'30"E); USNM 098948, 1: 178.6 mm SL (paratype of B. philippinus), west coast of Luzon, the Philippines (16°33'52"N, 119°52'54"E); USNM 098952, 2: 198.1-198.7 mm SL (paratypes of B. philippinus), Camp Overton Lt., Iligan

Bay; USNM 098953, 1: 143.3 mm SL (paratype of B. philippinus), between Leyte and Cebu, the Philippines (11°11'45"N, 124°15'45"E); USNM 098957, 8: 51.6-173.9 mm SL (paratypes of B. philippinus), Murcielagos Bay, the Philippines (08°46'N, 123°32'30"E); USNM 098960, 6: 112.1-137.7 mm SL (paratypes of B. philippinus), between Leyte and Cebu, the Philippines (11°10'N, 124°17'15"E); USNM 098974, 4: 62.8-124.6 mm SL (paratypes of B. philippinus), Pt. Togolo Lt. (08°47'N, 123°31'15"E); USNM 098976, 1: 82.0 mm SL (paratype of B. philippinus), Gulf of Boni, Celebes Island, Dutch East Indies (03°34'10"N, 120°50'30"E); AMS I.20118-019, 5: 143.6-161.5 mm SL, east of Wooli, N.S.W., Australia; NTM S.10998-002, 1: 90.1 mm SL, Indonesia; USNM uncat., 1: 103.8 mm SL, Gulf of Aden near Gubbat Kalwein, Somalia (11°10'N, 47°55'E).

5. OSTEOLOGY

The following descriptive osteology is based on two specimens of B. anatirostris – NSMT P44756 (SL 127.5 mm) and UF 20747 (SL 171.5 mm). All illustrations in this section are of UF 20747. Variation in the morphology of various osteological elements among different taxa is also discussed.

SKULL (Figs. 5.1, 5.2, 5.3 and 5.4)

The skull is long and narrow with very large orbits. Most of the dorsal cranial elements are covered by a thin overlying skin. The elements are thin and without any sculpturing, unlike the sculptured condition found in Percophis brasiliensis.

Skull roof

The skull is roofed by two pairs of dermal bones, the frontals and parietals, and by the median supraoccipital.

Frontal: The frontal (paired) is long and is very narrow for most its length anteriorly, resulting in a very narrow interorbital width. Along much of their length they overlap irregularly along the mid-line. Anteriorly, they are separated from each other and make contact with the mesethmoid laterally, while posteriorly, they are separated by the supraoccipital. Posterolaterally, they articulate with the parietals. The lateral portion of the frontal forms the dorsal border of the orbit; anterior to it is the lateral ethmoid, and posteriorly the dermosphenotic. A notch in the posterolateral section of the frontal accommodates the dermosphenotic.

Fig. 5.1. Left lateral view of the skull of Bembrops anatirostris. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.

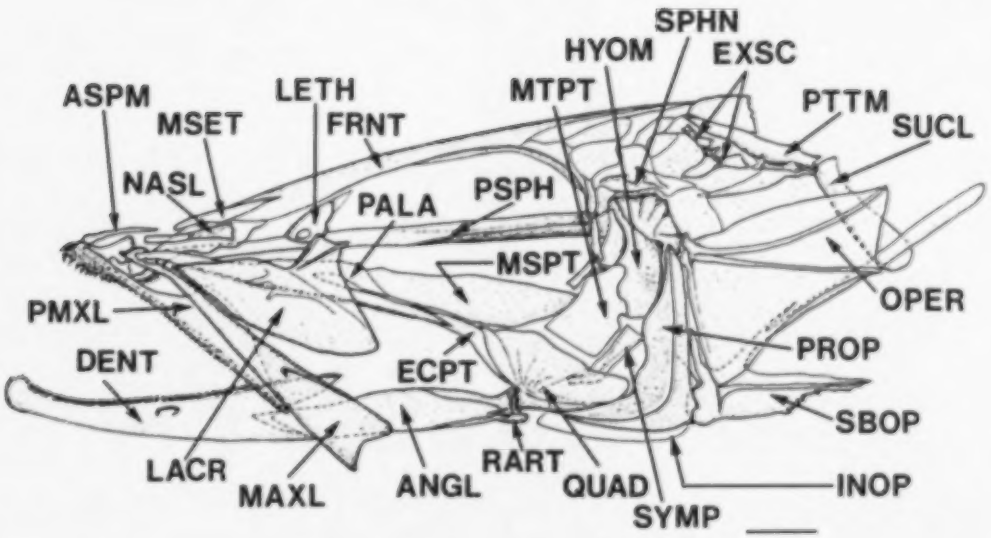

SPHN
HYOM
EXSC
ASPM
LETH
MTPT
PTTM
MSET
FRNT
SUCL
NASL
PSPH
PALA
MSPT
OPER
PMXL
PROP
DENT
ECPT
SBOP
LACR
RART
INOP
MAXL
ANGL
QUAD
SYMP

Fig. 5.2. Dorsal view of the skull of Bembrops anatirostris. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.

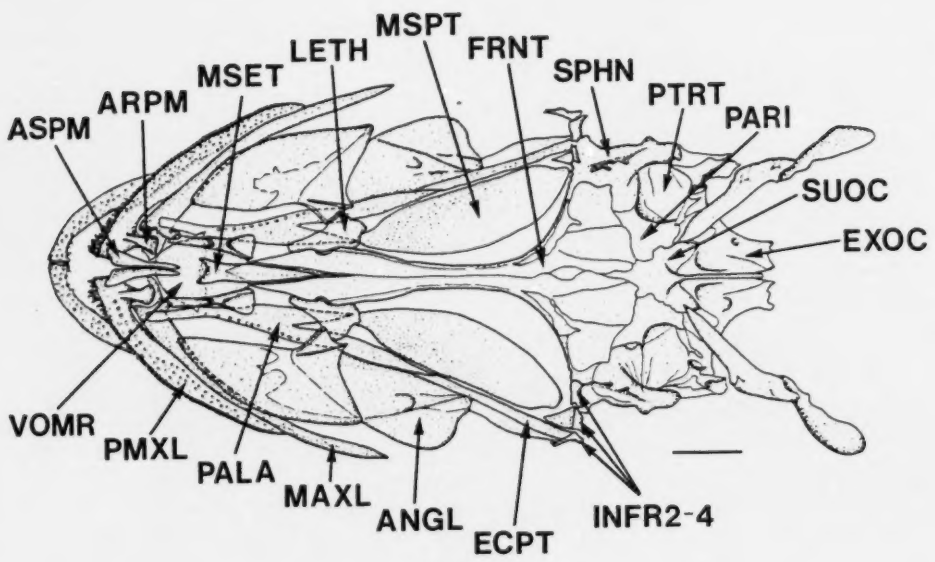

MSPT
LETH
FRNT
MSET
SPHN
ARPM
PTRT
ASPM
PARI
SUOC
EXOC
VOMR
PMXL
PALA
MAXL
ANGL
ECPT
INFR2-4

Fig. 5.3. Ventral view of the cranium of Bembrops anatirostris. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.

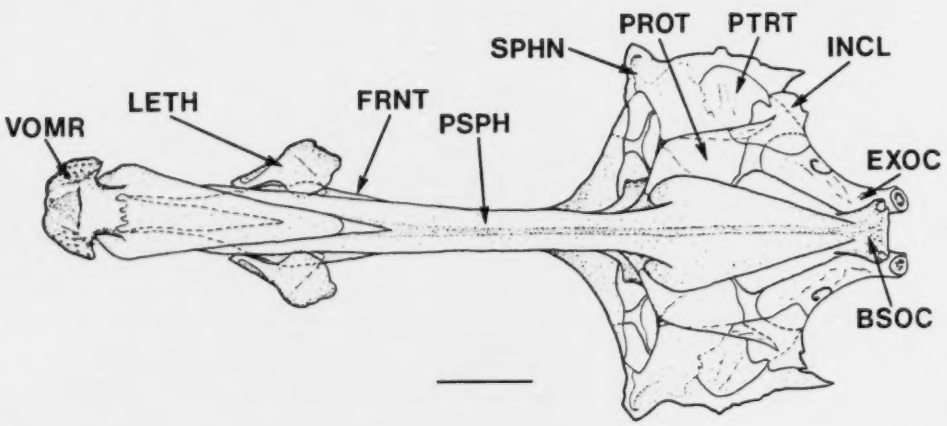
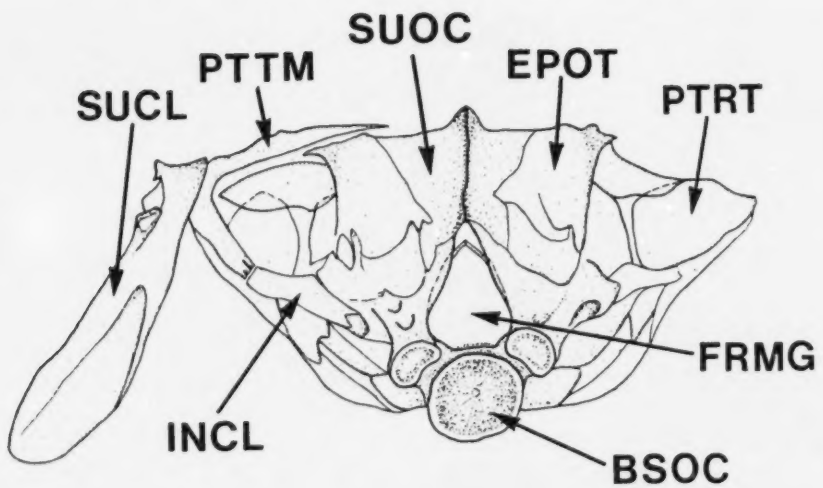

PROT
PTRT
SPHN
INCL
LETH
FRNT
VOMR
PSPH
EXOC
BSOC

Fig. 5.4. Posterior view of the cranium of Bembrops anatirostris, with posttemporal, and supracleithrum of the left side. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


SUOC
PTTM
EPOT
SUCL
PTRT
FRMG
INCL
BSOC

Parietal: The parietals are separated from each other by the medial supraoccipital. They articulate anteriorly with the frontals, anterolaterally with the sphenotics, posterolaterally with the pterotics, and posteromedially with the supraoccipital.

Supraoccipital: The supraoccipital covers the posterior dorsomedial portion of the skull. Its anterior end narrows into a triangular point and extends beneath the posterior end of the frontals. The posterolateral extension of the supraoccipital contacts the epiotics. The anterior tip of the posttemporal lies on the dorsal surface of the supraoccipital. Although the supraoccipital does not border the foramen magnum, a thin vertical plate extends down and contacts the exoccipitals at the top of the foramen magnum.

Ethmoid region

Nasal: The nasal (paired) is a tubular goblet-shaped bone with its posterior portion expanded laterally. It is very superficial, and loosely attached to the skin. Nerve foramina can be seen at its anterior and posterior ends.

Mesethmoid: The mesethmoid is well developed, and rectangular in shape with notches at both its anterior and posterior ends; the posterior notch is relatively deeper than the anterior one. It lies anterior and medial to the lateral ethmoids, and posteriorly articulates with the anterior edge of the frontals. It lies dorsal to the vomer, and its ventral surface is covered by the vomer.

Lateral ethmoid: The lateral ethmoid (paired) is somewhat triangular. The anterior end is narrower, and the posterior end expands laterally. The posterodorsal part of the lateral ethmoid meets the anterolateral edge of the supraorbital section of the frontal, attaching

underneath it. Ventrolaterally, it articulates with the lacrymal, and together they form the anterodorsal part of the orbit. It does not articulate with the mesethmoid.

Vomer (Fig. 6.2): The vomer is a somewhat triangular, wedge-shaped bone forming the anteriormost part of the neurocranium. It lies anteroventrally to the mesethmoid. Its triangular head is wide and concave ventrally. Its lateral edges are thicker than its medial part due to the presence of a groove along its medial surface. Numerous fine teeth are present only along the lateral edges. The medial groove is also present in Chrionema and Hemerocoetes, but absent in Percophis. As a result, in Percophis, the whole ventral surface of the head of the vomer is covered by numerous small teeth. The vomer has a gradually tapering posterior end, and a pair of laterally-directed small wings immediately posterior to the head.

Infraorbital series

The only elements corresponding to the infraorbital series in Bembrops are the paired lacrymals (= first infraorbital) and infraorbitals 2-4. The infraorbital series does not encase the lower margin of the orbit; there is a distinct gap between the lacrymal and second infraorbital. The elements are superficial and are formed by thin bones without any sculpturing.

The lacrymal is situated anterior and lateral to the lateral ethmoid, and together, they form the dorsolateral part of the orbit. The lacrymal articulates with the lateral ethmoid by a concave facet present on its narrowed dorsal end. Sensory nerve foramina are seen in its lateral surface. In Bembrops the lacrymal is triangular in shape and is the largest in size among the four infraorbital elements. Ventrolaterally, it lies dorsal to the maxilla and partially covers the dorsalmost part of the post-maxillary process of premaxilla. Its general

shape is similar in the four genera examined, except in Percophis the posterior end of each lacrymal is greatly extended to join the second infraorbital, and as a result, the infraorbital series completely encases the ventral margin of the orbit. In Hemerocoetes the lacrymal and the second infraorbital also articulate with each other, but the posterior extension of the lacrymal is not present. Instead, the orbit is reduced and infraorbitals 2-4 are longer.

Infraorbitals 2-4 are very small, tubular bones carrying the infraorbital canal through them. Together, they form part of the posterior margin of the orbit. The second infraorbital is usually slightly longer than the other two elements. The fourth infraorbital (= dermosphenotic) is found posterior to the posterolateral edge of the frontal, and anterior to a lateral projection of the sphenotic.

Otic and occipital regions

The bones of the otic and occipital regions are of varied origin. The supraoccipital is discussed in the skull roof section.

Epiotic: The epiotics are paired bones situated at the posterior end of the neurocranium. Medially, they contact the supraoccipital. They are separated from each other by the supraoccipital. Laterally, they are connected to the pterotics. Dorsally, they provide an articulating surface for the upper arm of the posttemporals.

Pterotic: The pterotic (paired) is somewhat elongate. It is bordered anterolaterally by the sphenotic, anteromedially by the parietal, and posteromedially by the epiotic. The pterotic and the epiotic together create a shallow open fossa. Laterally, the posterior end of the hyomandibular contacts the pterotic.

Sphenotic: Most of the dorsolateral part of the hyomandibular bone articulates anteriorly with the sphenotic (paired). The sphenotic forms the posterodorsal corner of the orbit. Dorsomedially, it articulates with the frontal anteriorly, and with the parietal posteriorly. It also makes contact with dermosphenotic dorsally, with the pterosphenoid and prootic ventrally. Some 2 or 3 small and thin bony projections extend out from its dorsolateral side.

Intercalar: The intercalar (paired) is a small elongated bone situated toward the posterior end of the skull. Laterally, it articulates with the ventral process of the posttemporal. Dorsally, it makes contact with the basioccipital.

Exoccipital: The exoccipitals are more or less triangular elongated posteriorly and form part of the border of the foramen magnum. The posterior end carries a facet which articulates with the first vertebra. The exoccipitals articulate with the basioccipital ventromedially and with the anteroventral process of the supraoccipital dorsally.

Basioccipital: The basioccipital ends posteriorly in a centrum-like condyle, which serves as the articular point for the first vertebra. The basioccipital bone forms a ventral dome for the neurocranium. Its anterior edge is covered by the posterior extension of the parasphenoid.

Prootic: The prootic (paired) is triangular in shape, and forms part of the floor of the neurocranium. Medially, it is separated by the parasphenoid. It articulates with the exoccipital posteromedially. It also makes contact with the sphenotic anterolaterally, and with the pterotic laterally.

Parasphenoid: The parasphenoid is long and narrow, and ventrally covers the median portion of the basioccipital and prootics. Just anterior to the prootics, there are two small lateral projections. Anteriorly, this bone extends as a narrow median bone and terminates with a bifurcation which serves as the articulating surface for the vomer and the mesethmoid.

UPPER JAW (Figs. 5.1 and 5.2)

Two paired bones form the upper jaw, the premaxillae and maxillae. Supramaxillae are absent. The premaxillae and maxillae overlap in both lateral and dorsal aspects.

Premaxilla: The premaxilla is elongated with three distinct processes: the ascending process, the articular process, and the postmaxillary process. The ascending process is short and slender, slightly broader at the base, and ends in a pointed tip. It is situated vertically on the premaxilla and loosely connected via tendons. It lies parallel to its counter part along the mid-line. The articular process articulates with the maxilla between the anterolateral process and the dorsomedial process of the maxilla and is more or less thumb-shaped. The postmaxillary process is wide at its base, and has a flat dorsal edge. The postmaxillary process lies beneath and mesial to the maxilla and the lacrymal over most of its length. There are numerous fine teeth along most of the length of the premaxilla, with approximately 32 relatively large teeth in the symphysial area.

Maxilla: The maxilla is toothless, more or less flat, except anterodorsally where it is constricted into a cup-like articular facet embracing the head of the premaxilla, relatively wide posteriorly, with a notch at the posterior end. Anteriorly, it has two processes – the anterolateral and the dorsomedial process. The articular process of the premaxilla articulates

between these two processes. The maxilla laterally covers most of the premaxilla with the ventralmost portion exposed. The anterior end of the palatine sits dorsally on the maxilla just lateral to the anterolateral and dorsomedial processes. The nasal lies just posterior to the dorsomedial process of the maxilla, although it does not make direct contact.

LOWER JAW (Figs. 5.1 and 5.2)

The lower jaw is robust and consists of paired dentaries, angulars and retroarticulars.

Dentary: The paired element is curved mesially, especially anteriorly, where it articulates via a symphysial joint to its complement. The dentary bears numerous small teeth along its length. A prominent foramen can be identified just below the tooth row on the lateral side. The symphysial tip of the dentary is slightly raised. Posteriorly, it consists of dorsal and a relatively smaller ventral prong. The anterior process of the angular articulates with the dentary at this point of bifurcation.

Angular: The angular is the second largest of the lower-jaw elements. The dorsal, larger limb slides into the angle formed by the dorsal and ventral prongs of the dentary, and the ventral limb extends toward the ventral fork of the dentary.

Retroarticular: The retroarticular is a small ossification, and articulates with the angular at its posteroventral corner by fibrous tissue. It also contacts the interopercle by means of a ligament.

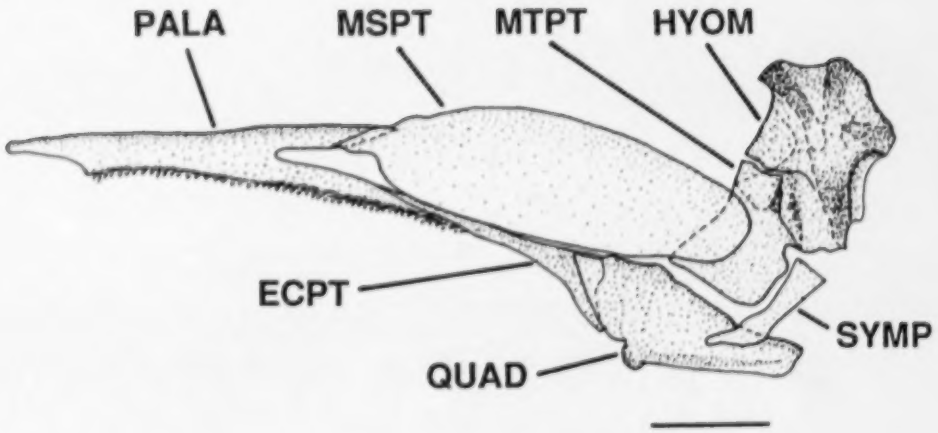
SUSPENSORIUM (Figs. 5.1 and 5.5)

The suspensorium is composed of seven bones: the hyomandibular, metapterygoid, mesopterygoid, ectopterygoid, palatine, quadrate and symplectic.

Hyomandibular: The dorsal part of the hyomandibular has two distinct heads – the anterior head articulates with the sphenotic and the posterior one with the pterotic. A lateral crest is present, which runs from the anterodorsal corner to the area adjacent to the dorsal tip of the preopercle. This character is also found in Chrionema and Hemerocoetes, whereas Percophis has an anteriorly directed spur in the same area of the hyomandibular. A small opening is also found in the posterolateral area in some species of Bembrops (B. filifera, B. gobioides, B. heterurus and B. macromma), and the same is true for Percophis and Chrionema. The opening is lost in other Bembrops species examined for osteology (B. anatirostris, B. curvatura, B. morelandi and B. platyrhynchus) and also in Hemerocoetes.

Metapterygoid: The metapterygoid is located ventral to the hyomandibular. It also makes contact with the symplectic posteroventrally and with the mesopterygoid anteriorly with cartilage between. It is a rectangular bone with a straight dorsal edge in two species of Bembrops (B. filifera and B. morelandi), in Percophis, and in Chrionema. The other six species (B. anatirostris, B. curvatura, B. gobioides, B. heterurus, B. macromma and B. platyrhynchus) examined, and also Hemerocoetes, show development of a pointed tip on the dorsal side. There is a prominent notch present posteriorly in the area where the metapterygoid meets the ventral part of the hyomandibular. The ventral part of this bone is in the same plane as the dorsal edge of the quadrate. There is a distinct gap between these two bones.

Fig. 5.5. Internal view of the suspensorium of right side of Bembrops anatirostris. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


PALA
MSPT
MTPT
HYOM
ECPT
SYMP
QUAD

Mesopterygoid: The mesopterygoids are paired dermal bones formed in the middle part of the pterygopalatine arch. The mesopterygoid on each side is elongated, flat, and oval in shape; the anterior end is tapered where it articulates with the lateral arm of the palatine. It is also associated with three other bones: the metapterygoid posteriorly, the quadrate posterolaterally, and the ectopterygoid anterolaterally. The mesopterygoid forms the floor of the orbit and the roof of the mouth. The posterior end of the mesopterygoid is not curved upward and does not contact the neurocranium in Bembrops, Chrionema and Percophis, whereas although it is slightly curved upward but does not reach the neurocranium in Hemerocoetes pauciradiatus.

Ectopterygoid: The ectopterygoid (paired) is a toothless, slightly bent, elongate bone, articulated anteriorly with the posterior margin of the arm of the palatine. It articulates with the anterodorsal corner of the quadrate via the posterior quadrate fossa and lies very close to the lateral margin of the mesopterygoid.

Palatine: The palatine (paired), the anteriormost bone of the suspensorium, develops from a mixed origin of ossifications, endochondral and dermal, in modern teleosts (Rojo, 1991). In Bembrops, each palatine is long and triangular in shape with narrow anterior and wider posterior ends. Anteriorly, it has an elongate, slightly curved process which slides into a transverse groove on the dorsal surface of the maxilla just behind its anterolateral and dorsomedial processes. Posteriorly, the palatine sends off two rami; the lateral ramus is longer than the medial one and articulates with the anterior end of the ectopterygoid. The medial ramus slightly overlaps the anterior surface of the mesopterygoid. In Percophis, Chrionema and Hemerocoetes, there is a distinct bony lamina between the two rami which is absent in all species of Bembrops. Anterodorsally, the palatine lies ventral to the lacrymal and lateral ethmoid without any direct articulation with them. The palatine is a tooth-bearing

bone in Percophis, Chrionema and Bembrops. Hemerocoetes lacks teeth on its palatine. In Percophis, Chrionema and most species of Bembrops, there are more rows of teeth at the anterior end. B. anatirostris and B. gobioides have only one or two rows of teeth anteriorly, and three or four rows at the posterior end.

Quadrate: The quadrate (paired) is triangular and acts as a pivot for the mandible. It articulates with the articular facet of the angular through the condyle present at its apex. The anterior end of the quadrate overlays the posterior quadrate fossa of the ectopterygoid. Dorsally and dorsomedially, it is distinctly separated by small gaps from the mesopterygoid and the metapterygoid. The posteroventral edge of the quadrate lies over the dorsal surface of the horizontal arm of the preopercle. The anteroventral part of the symplectic lies on a depression on the inner face of the quadrate.

Symplectic: The ventral portion of the symplectic lies medially behind the quadrate. It has a rod-like, cartilage-capped terminal end. It is slightly expanded dorsally and lies near the posterior notch of the metapterygoid. In B. curvatura, B. filifera, and B. platyrhynchus the dorsal edge of the symplectic lies near the dorsal margin of the metapterygoid notch .

OPERCULAR REGION (Figs. 5.1 and 5.2)

Opercle: The opercle is a large, more or less triangular, mostly flat and thin bone. There are two crests ending in spines present on the opercle pointed posteriorly; the upper spine is oriented upwards at an angle of approximately 30° while the lower spine is horizontal. The opercle articulates with the hyomandibular, just below the posterior end of the dorsal part of that bone. The articulating surface is characterized by a raised, knob-like prominence.

Subopercle: Lying ventral and medial to the opercle is the subopercle. The subopercle is bifurcated into a long, narrow, flattened upper limb, which extends beyond the opercle, and a short, relatively wide, crested lower limb. One subopercular spine terminates the lower limb. The posteroventral margin is serrated in some specimens.

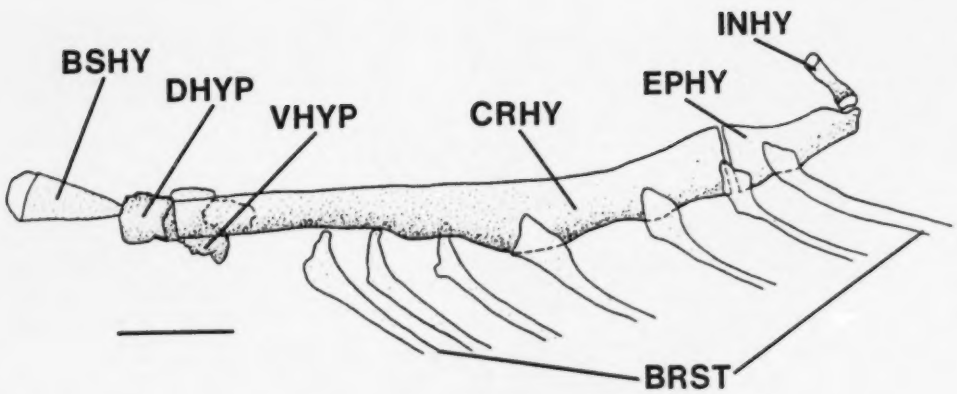
Preopercle: The preopercle is crescent-shaped with a slightly thickened ridge along most of its length. The dorsal limit of the preopercle articulates by fibrous tissue with the posterior end of the lateral crest of the hyomandibular. Its posterior edge lies parallel to the anterior margin of the opercle. Ventrally, the preopercle overlies the dorsal edge of the interopercle along about most of the length of the former. Its anterodorsal edge fits into the medial face of the quadrate.

Interopercle: The interopercle is thin, oblong, tapering anteriorly, broad posteriorly. The interopercle is found closely associated with the medial side of the preopercle, but it extends slightly beyond the ventral border of the preopercle. Anteriorly, it is connected to the retroarticular by a ligament. B. anatirostris, B. gobioides and B. macromma have a tiny spine-like extension at the posterodorsal tip of the interopercle.

HYOID ARCH (Figs. 5.1 and 5.6)

The hyoid arch consists of the following elements (from dorsal to ventral): hyomandibular, symplectic, interhyal, epihyal, ceratohyal, dorsal hypohyal, ventral hypohyal, basihyal, and urohyal. The hyomandibular and the symplectic are discussed above in the suspensorium section.

Fig. 5.6. Lateral view of the hyoid apparatus of left side of Bembrops anatirostris. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


INHY
BSHY
DHYP
EPHY
VHYP
CRHY
BRST

Interhyal: Each interhyal is a short columnar bone with its distal end more expanded than the proximal end. It is connected via a cartilaginous tip to the hyomandibular proximally and to the posterodorsal end of the epihyal distally.

Epihyal: The epihyals are paired bones, more or less triangular (apex posteriorly), and loosely articulated with the posterior end of the ceratohyal. The posterodorsal articulating surface of the epihyal shows a distinct notch in Percophis, Chrionema and Hemerocoetes. Interspecific variation is observed in Bembrops. The notch is absent in B. curvatura, B. heterurus, and B. platyrhynchus.

Ceratohyal: The ceratohyals are paired, long, rounded stout bones. Each ceratohyal narrows anteriorly and articulates with the dorsal and ventral hypohyals. Posteriorly, it articulates with the epihyal by a straight suture.

Hypohyal: The dorsal and ventral hypohyals articulate with one another and with the anterior ceratohyals. The dorsal hypohyal also articulates with the basihyal via a ligamentous connection. The ventral hypohyal also articulates with the basihyal. The hypohyals of two sides are separated from each other by the medial basihyal.

Basihyal: The basihyal is a single bone that lies at the anterior end of the branchial region and extends forward toward the tip of the mouth. The basihyal is connected to the anterior end of the first basibranchial. Dorsally, the basihyal is triangular, widest anteriorly and narrows gradually toward its posterior end where it expands slightly; the expanded anterior margin is cartilaginous. The shape of this bone is variable within Bembrops. In B. curvatura, B. filifera and B. platyrhynchus the anterior end is distinctly wider and the length is shorter compared to the other species of Bembrops and the outgroups.

Urohyal (Fig. 6.6): The urohyal is a single median bone composed of a vertical plate medially and a horizontal plate ventrally. Anteriorly, both plates merge into a narrow margin where it bifurcates slightly into two prongs serving as the point of attachment for a pair of ligaments extending from the ventral hypohyals. The vertical plate is deep in most species of Bembrops, except in B. macromma and B. heterurus where the vertical plate is expanded posteriorly along its mid-line. The urohyal is also attached to the basihyal with loose connective tissue.

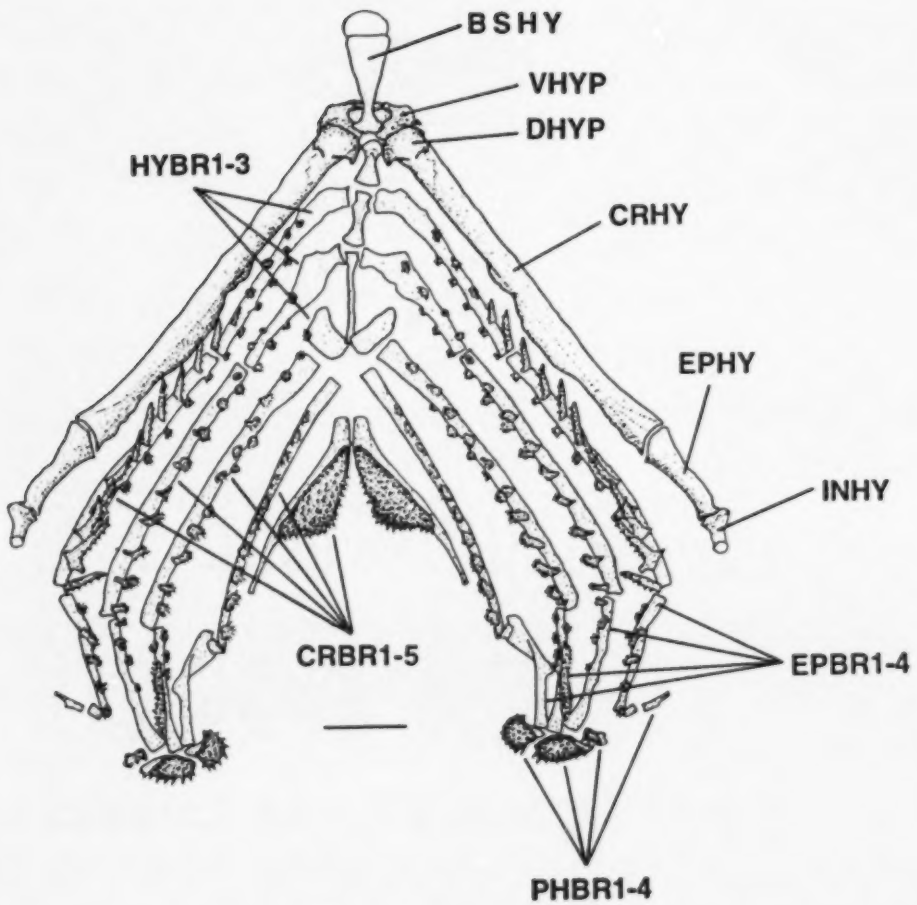
Branchiostegal rays: There are seven branchiostegal rays. The ceratohyal supports the anterior five branchiostegal rays. The sixth ray articulates in the area of the ceratohyal-epihyal junction and the last ray is supported by the epihyal. All species of Bembrops share this character with Chrionema. In Percophis and Hemerocoetes, the sixth ray is distinctly located on the epihyal. The third branchiostegal ray shows a distinct intergeneric variation among the four genera studied. Its proximal end is wider in all species of Bembrops compared to that in the other three genera.

BRANCHIAL ARCHES (Fig. 5.7)

The branchial arches are composed of basibranchials, hypobranchials, ceratobranchials, epibranchials, and pharyngobranchials. Among these elements, only the basibranchials are unpaired and located medially. The epibranchials and pharyngobranchials, the dorsal gill arch elements, are suspended from the neurocranium and are connected to the ventral gill arch elements laterally.

Basibranchials: The basibranchials consist of three anterior ossified elements and one cartilaginous element posteriorly. The first basibranchial is the smallest among the three

Fig. 5.7. Dorsal view of the branchial apparatus of Bembrops anatirostris; branchiostegal rays, and cartilages (except basihyal cartilage) not shown. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


BSHY
VHYP
DHYP
HYBR1-3
CRHY
EPHY
INHY
CRBR1-5
EPBR1-4
PHBR1-4

ossified elements and is somewhat hourglass shaped in dorsal profile. The third basibranchial is the longest and the narrowest . The basibranchials articulate end to end and anteriorly with the posterior tip of the basihyal. The cartilaginous fourth basibranchial is diamond-shaped and occupies a position central to the paired third hypobranchials anteriorly and fourth ceratobranchials posteriorly. The first basibranchial articulates laterally with the dorsal hypohyal at its anterior end and with the first hypobranchial posteriorly. The second and third basibranchials articulate laterally with the hypobranchials both anteriorly and posteriorly.

Hypobranchials: There are three pairs of hypobranchials lateral to the basibranchials and at the anteromesial ends of the first three ceratobranchials. The first and second are longer and tubular with the anterior end angled somewhat posteriorly. The third hypobranchial is smallest, more medially located, and more or less rectangular in shape. Anteriorly, it narrows into a tubular extension in most species of Bembrops and in the outgroups; this extension is absent in B. anatirostris, B. gobioides and B. heterurus.

Ceratobranchials: There are five pairs of ceratobranchials. The first four pairs are thin, and long, and somewhat concave ventrally. All four ceratobranchials are ornamented with gill rakers. The gill rakers on the first ceratobranchial are much longer and more slender, while those on the second, third, and fourth are relatively short and stumpy. The first three ceratobranchials articulate with the three hypobranchials mesially, while the fourth articulates with the cartilaginous fourth basibranchial anteriorly. The posterior end of the fourth ceratobranchial curves dorsally to meet the fourth epibranchial. The fifth ceratobranchial is approximately two-thirds the length of the fourth ceratobranchial but much wider in its middle area. It is somewhat oval in shape with a smaller anterior tubular extension and a longer posterior tubular extension. It bears only teeth, no gill rakers.

Anteriorly, the cartilage-tipped head approaches the medial head of the fourth ceratobranchial. Except for the anterior and the posterior tubular extensions, the fifth ceratobranchial is covered with numerous small to medium sized teeth. Teeth found along the inner curvature of the bone are relatively large and somewhat recurved.

Epibranchials: All four epibranchials articulate with their respective ceratobranchials laterally and with the pharyngobranchials posteromedially. Cartilage is present at both their anterior and posterior ends. The first epibranchial consists of narrow proximal and distal portions and a posterodorsally directed, cartilage-tipped, uncinate process. The uncinate process is broad at both the proximal and distal ends and is connected to the second pharyngobranchial by a short cartilage. In overall shape the second epibranchial is similar to the first. The uncinate process is much smaller. It is also more closely located to the third pharyngobranchial than to the second. The uncinate process on the third epibranchial is narrower and extends medially toward the fourth epibranchial. The uncinate process on the fourth epibranchial is more proximally located and is wider at its base. A short extension makes a secured attachment with the third epibranchial via cartilage.

Pharyngobranchials: There are four pharyngobranchials corresponding to four epibranchials. All of them have cartilaginous tips at their proximal and distal ends. The first pharyngobranchial is relatively smaller in length than the other three and bears no teeth. The other three pharyngobranchials bear few to numerous small teeth on their lateral and medial surfaces. They are semi-oval or tear-drop shaped.

There are numerous thin tooth plates present on the hypobranchials, ceratobranchials, and epibranchials. Each tooth plate bears small, closely set teeth, arranged in rows. A large, somewhat oval tooth-plate lies on the third epibranchial.

VERTEBRAE (Fig. 5.8)

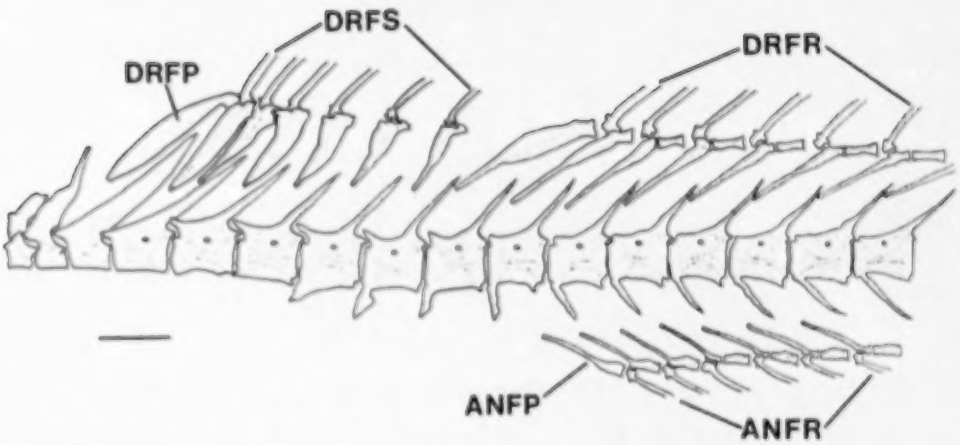
The vertebral number in the 13 species of Bembrops examined, including the urostyle, is 27 or 28 (98% of the specimens examined have 28), with 9 precaudal vertebrae and 18 or 19 caudal vertebrae. Miller and Jorgensen (1973) reported 30 vertebrae in B. gobioides, based on their examination of four specimens. My observation does not support this.

The first vertebra is smallest with a short centrum that fits securely against the basioccipital and exoccipitals. The neural spine of the first vertebra is shorter in length and broader along its dorsoventral axis and it has a larger neural canal.

Each of the other precaudal vertebrae has a well-developed neural spine directed posterodorsally and paired prezygapophyses directed anterodorsally. The prezygapophyses are well developed anteriorly, extending almost to the neural spine of the preceding element, and decrease in size posteriorly. Posterior to the neural spine are the small postzygapophyses. The neural spine of the third vertebra is expanded in the anterior-posterior plane at its proximal end. The general trend of the neural spines is to become progressively more slender toward the posterior end of the vertebral column. Predorsal bones are absent in Bembrops, Chrionema and Hemerocoetes; there are five well-developed predorsal bones in Percophis.

Both epipleural and pleural ribs are present. There are 10 pairs of epipleural ribs associated with the first 10 vertebrae. The epipleural ribs are situated high on the anterior four vertebral centra and there is a gradual move to a more ventral position in the subsequent vertebrae. Each rib has a more or less rounded proximal tip, which is loosely attached to the body of the vertebrae and is directed posteriorly toward the lateral line. The last four pairs are greatly reduced in length. There are four pairs of pleural ribs associated with the third to sixth epipleural ribs. The pleural ribs are relatively weak and arise midway

Fig. 5.8. Left lateral view of the anterior 16 vertebrae and the dorsal and the anal fin skeleton of Bembrops anatirostris; ribs not shown. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


DRFS
DRFP
DRFR
ANFP
ANFR

along the length of the epipleural ribs. Nelson (1986) reported a similar unusual epipleural-pleural relationship in the trichonotids. The pleural ribs are absent in Hemerocoetes.

Haemal spines and arches are developed ventrally on the caudal vertebrae, and parapophyses are also lacking. Generally, the last two to three precaudal vertebrae (vertebrae 7 to 9) are transitional vertebrae. They have an incomplete or very small haemal arch; they are also characterized by well-developed ventral postzygapophyses; the ventral prezygapophyses are relatively weakly developed compared to the preceding vertebrae.

Caudal vertebrae are generally monomorphic. Both pre-and postzygapophyses are smaller. All caudal vertebrae have an enclosed haemal arch and spine with small haemal pre- and postzygapophyses. A haemal canal, beginning at the first caudal vertebra, runs through the haemal arches. Posteriorly, toward the caudal fin, the neural and haemal spines become increasingly bent posteriorly.

CAUDAL SKELETON AND FIN (Fig. 5.9)

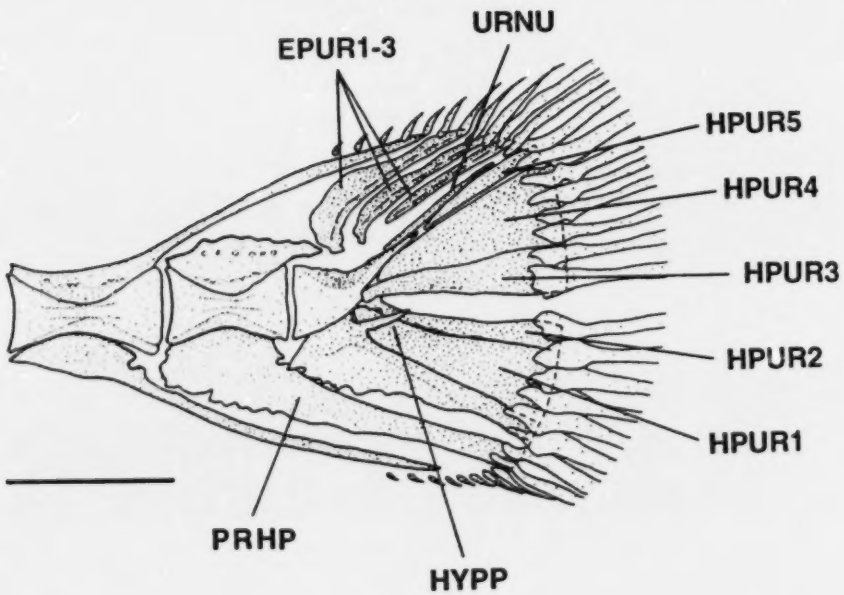
The caudal skeleton of Bembrops includes two lower hypural bones, three upper hypural bones, a parhypural anterior to the first hypural with a well developed hypurapophysis, one long uroneural, and three epurals.

The terminal half-centrum, representing the first pre-ural centrum, is situated anterior to the hypurals. The half centrum curves dorsally along the dorsal edge of the fourth hypural and nearly meets the anterior end of the fifth hypural bone.

The second pre-ural vertebra has a well-developed haemal arch and spine but the neural arch and spine are much reduced.

Hypurals: The two hypurals of the lower lobe are separate though tightly bound as are the three of the upper lobe in Bembrops, Chrionema and Percophis; they are not fused into dorsal and ventral hypural plates as they are in Hemerocoetes.

Fig. 5.9. Left lateral view of the caudal skeleton of Bembrops anatirostris. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


URNU
EPUR1-3
HPUR5
HPUR4
HPUR3
HPUR2
HPUR1
PRHP
HYPP

The parhypural is well developed and very closely appressed along the ventral edge of the first hypural. It articulates with the terminal half-centrum, but is not fused with it. It ends posterodorsally with the hypurapophysis, a spike-like projection, with a narrow distal tip.

In B. anatirostris, the first and second hypurals are attached to each other along most of their length. Most of the other species show a similar degree of attachment of the two elements. In B. caudimaculata and B. heterurus the two bones are attached to each other only at their anterior and posterior tips, leaving a distinct gap in the middle portion; they share this feature with Percophis. The third and fourth hypurals show complete attachment to each other in Bembrops, Chrionema and Percophis. The fifth hypural is smaller, reduced almost to a thin splint, and approximately two-third the length of the fourth hypural. A very thin, tubular uroneural is present anterodorsal to the fifth hypural.

Epurals: There are three epural bones, the first being the longest and widest. It is situated very close to the neural spine of the second pre-ural vertebra. The proximal end of the first epural has a blunt tip in most species of Bembrops, Chrionema, Percophis and Hemerocoetes. The tip is pointed in B. curvatura, B. filifera, B. heterurus and B. platyrhynchus.

Fin rays: The first and second hypurals bear three unbranched and five branched principal caudal rays, and the third, fourth and fifth bear six branched and four unbranched caudal rays in B. anatirostris. The number of unbranched principal caudal rays shows intra- and interspecific variation.

The number of dorsal procurrent rays varies between 2 to 15 in Bembrops and the outgroups. The ventral procurrent rays vary from 1 to 13. Hemerocoetes has the lowest number of both dorsal and ventral procurrent rays. All species of Bembrops and Percophis

have 7 to 11 dorsal and 5 to 9 ventral procurrent rays. Chrionema shows the highest number, 13 to 15 dorsal and 11 to 13 ventral procurrent rays.

DORSAL FIN (Fig. 5.8)

Bembrops has two dorsal fins. There are six spines in the first dorsal fin, a character it shares with Chrionema. Percophis brasiliensis has nine spines in the first dorsal fin. Hemerocoetes pauciradiatus lacks a spinous first dorsal fin. There are 13-17 branched rays in the second dorsal fin.

There are seven pterygiophores associated with the six dorsal spines. All pterygiophores of the first dorsal fin in Bembrops are incomplete, that is, they lack three separate elements. The middle elements of the first four pterygiophores are fused to the proximal elements, and together they form the basals. Distal elements are also absent in the first dorsal fin. The basal radials are somewhat dagger-shaped bones; they show a gradual decrease in size toward the posterior end. The first dorsal spine is associated with two pterygiophores, the anterior one situated in front of the neural spine of the third precaudal vertebra. The second and third pterygiophores are situated between the neural spines of the third and the fourth precaudal vertebrae. The dorsal spines are long and slender. The anterior first three spines are elongate in a number of species of Bembrops; the second or third spine is elongated in larger males (SL > 170 mm) of B. anatirostris; the first spine is elongated in many adult specimens of both sexes of B. filifera; the second spine is elongated in some specimens of B. macromma; the first spine shows some evidence of elongation in larger specimens of B. morelandi; the first spine is elongated in many specimens of B. nematopterus and B. platyrhynchus. The middle elements are fused to the proximal elements in the anterior two pterygiophores associated with the first and second ray of the second dorsal fin. The remaining pterygiophores are complete with all three

elements. There is a one-to-one relationship between the soft rays of the second dorsal fin and the pterygiophores, and between the neural spines and the pterygiophores. There are seven proximal elements present between the spinous and the soft dorsal fins of Percophis, while no free pterygiophore is present in Bembrops and Chrionema in the area between the spinous and the soft dorsal fins. All soft rays are branched. The last ray consists of two branched elements.

ANAL FIN (Fig. 5.8)

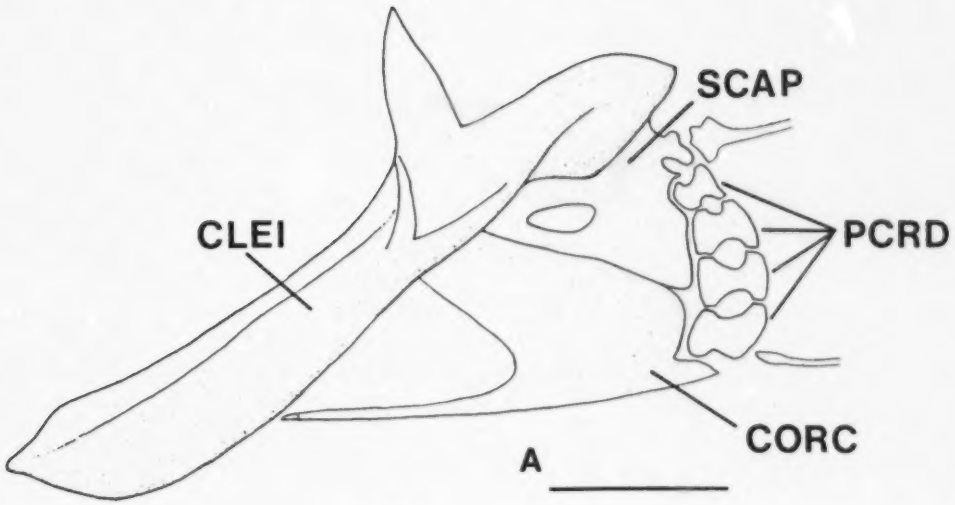
The anal fin consists of 14 to 18 soft rays, only the last three or four being branched, and each ray is associated with a pterygiophore. The first proximal anal element extends toward the first caudal vertebra (vertebra 10). The three anteriormost rays are associated with fused proximal and middle elements. Both proximal and middle elements are present along with the rest of the fin rays. The one-to-one relationship between the pterygiophores and the haemal spines is not present. The last ray of the anal fin also consists of two branched elements.

PECTORAL GIRDLE AND FIN (Figs. 5.1, 5.4, and 5.10)

The pectoral girdle of Bembrops, as in most teleosts, consists of the dermal extrascapular, posttemporal, supracleithrum, cleithrum, and postcleithrum, and the endochondral scapula, and coracoid.

Extrascapular: The extrascapular (paired) (Fig. 5.1) is a somewhat Y-shaped tubular bone, situated dorsolaterally behind the roof of the skull. The medially extended single arm of this

Fig. 5.10. Left lateral view of the pectoral girdle (A), and postcleithra (B) of Bembrops anatirostris. Horizontal bar for Fig. 5.10A equals 5 mm and for Fig. 5.10B equals 2 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


SCAP
CLEI
PCRD
CORC
A

B

bone is divided into two elements along its length. The proximal arm receives the sensory canal from the posttemporal and has two pores on its lateral side.

Posttemporal: The posttemporal (paired) (Figs. 5.1, 5.2 and 5.4) is a V-shaped bone, situated dorsolaterally on the posterolateral corner of the skull. The longer dorsal arm lies very close to the supraoccipital. The lower arm, which points anteroventrally, is about half the length of the upper arm, and articulates securely with the dorsal edge of the intercalar. Medially, it overlaps the dorsal surface of the posterolaterally directed surface of the epiotic. There is a well-developed posteriorly directed spine at the junction of the two arms. Posteroventrally, the bone articulates with the supracleithrum.

Supracleithrum: The supracleithra are a pair of oblong, flat dermal bones that are connected to the posttemporal dorsally and the cleithrum ventrally. They contain part of the continuation of the sensory canal leading from the posttemporal to the lateral line. Each supracleithrum is broadest at the mid-point and ventrally. The morphology of this element is very similar in all species of Bembrops.

Cleithrum: The cleithrum (paired) is the largest of the pectoral elements and forms a major part of the lateral face of the girdle. It is roughly Y-shaped with a large ascending ramus and a pair of smaller horizontal branches directed anteroposteriorly. Each ascending forms a slight sigmoid curve, is broader laterally, and ends in an almost pointed tip. Ventrally, the tips of two sides securely attach to each other at the mid-ventral line. The dorsal anterior arm is narrower than the posterior arm.

Postcleithrum: There are two postcleithra on each side, a dorsal and a ventral one arising along the medial side of the coracoid. The broad dorsal postcleithrum is loosely attached to

the scapula at its posteromedial corner. The narrow, rod-like ventral postcleithrum is somewhat posteriorly directed, and hangs loosely within the tissue behind the area of articulation of the pectoral rays. Pietsch (1989), and Pietsch and Zabetian (1990) reported that a postcleithrum is absent in the percophids. However, all four percophid genera that I have examined possess two postcleithra.

Scapula: The scapula (paired) articulates with the cleithrum along the dorsal third of its posterior margin, and is bordered by the coracoid ventrally. It is a roughly triangular flat bone. An oval scapular foramen lies within the scapula itself, with its long axis running in an anterior-posterior direction. The posterodorsal corner of the scapula has a saddle-shaped condyle with which the first pectoral fin ray articulates.

Coracoid: The coracoid (paired) has two distinct arms extending anteriorly toward the cleithrum. The upper arm is broad and articulates with the cleithrum. The lower arm is very narrow and is directed anteroventrally with a distinct cartilage tip that lies very close to the posteroventral edge of the cleithrum. There is a small process at the posteroventral corner of the coracoid.

Radials: There are four hour-glass shaped pectoral radials fitted into a recess in the posterior edge of the borders of the scapula and coracoid. The dorsal three are somewhat smaller than the fourth radial.

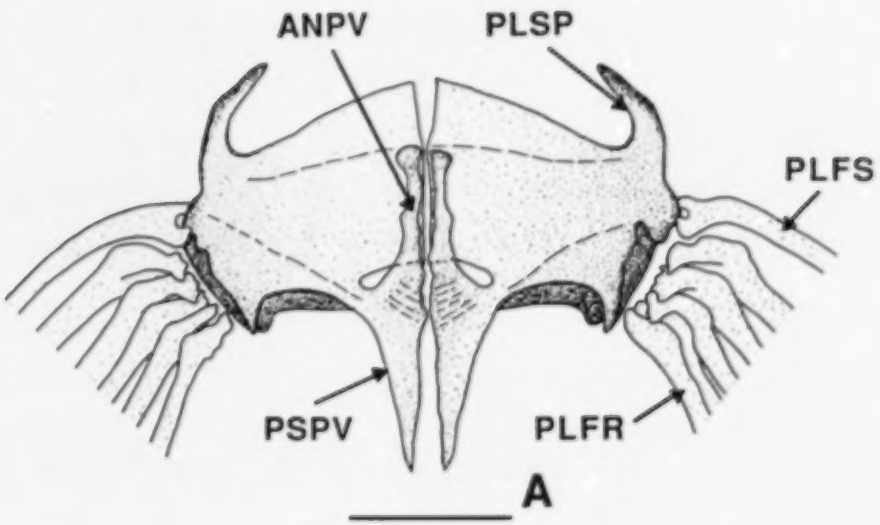
Fin rays: In Bembrops, there are 17-26 segmented, branched pectoral rays. The dorsalmost ray articulates with the saddle-shaped condyle of the scapula at its posterodorsal corner.

PELVIC GIRDLE AND FIN (Fig. 5.11)

The pelvic girdle consists of a large pair of laterally expanded basipterygia, which lie between the anteroventral margins of the cleithra. The basipterygia are narrowly separated from each other medially by cartilage. The rachis or crest is slightly tubular, and divides the basipterygium into two unequal portions. In Bembrops, Chrionema and Hemerocoetes, the rachis is oriented more or less perpendicular to the body axis. The basipterygium is more anteroposteriorly extended in Percophis, and as a result the rachis is situated at an angle to the body axis (Fig. 6.16A). Two anterior processes, located on the dorsal and ventral side, develop on each basipterygium at its posteromedial margin. Posteriorly, the ventral anterior process elongates into a posterior process. The length of the anterior and posterior processes show variation among different species of Bembrops and most of the outgroups. The anterior process is long in B. anatirostris and B. gobioides. B. curvatura and B. platyrhynchus are characterized by short posterior processes. Both anterior and posterior processes are absent in Hemerocoetes. In lateral view, the posterodorsal portion of the basipterygium rises in a broad dorsal process. A long, medially curved pelvic spur emerges from the anterolateral margin of each basipterygium in Bembrops, Chrionema and Hemerocoetes. The pelvic spur is relatively short in Percophis. A wide lateral process is present at the posterolateral edge of the basipterygium.

All four percophid genera have one spine and five segmented branched rays in the pelvic fin. The pelvic spine is relatively short and securely attaches itself to the lateral process. The pelvic rays are attached to basipterygium via ligaments.

Fig. 5.11. Ventral view (A) and left lateral view (B) of the pelvic girdle of Bembrops anatirostris. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


ANPV
PLSP
PLFS
PSPV
PLFR
A

PLSP
B

6. PHYLOGENETIC ANALYSIS

The goals of this section are to examine the monophyly of the genus Bembrops and to provide a working phylogenetic hypothesis of the interrelationships of the species included in the genus.

In the following discussion of relationships, each character is followed by a number in square brackets [ ] which refers to the sequence they were entered in the data matrix and also presented in the cladograms.

MONOPHYLY OF THE GENUS

Nelson (1984) divided the family Percophidae into three subfamilies (Table 1.1). The subfamily Percophinae contains a single monotypic genus, Percophis. Bembrops was included in the subfamily Bembropinae along with Chrionema, and it was suggested that the two genera together form a natural group (Iwamoto and Staiger, 1976). The third subfamily Hemerocoetinae consists of nine genera. A phylogenetic analysis was performed to test the monophyly of Bembrops in which three other genera (Percophis, Chrionema and Hemerocoetes) representing all three subfamilies were used as outgroups. By using these other members of the family, I have tried to avoid the danger of too heavy a reliance on a single outgroup.

The cladogram depicted in Fig. 6.1 represents the hypothesis of relationships of the four genera. A subset of the original data matrix (see Table 3.1) involving the first 31 characters produced a single cladogram with a length of 35 steps and a consistency index of 0.943. This data subset was useful for describing relationships of the four genera. The results were identical with both heuristic and branch-and-bound options. The run

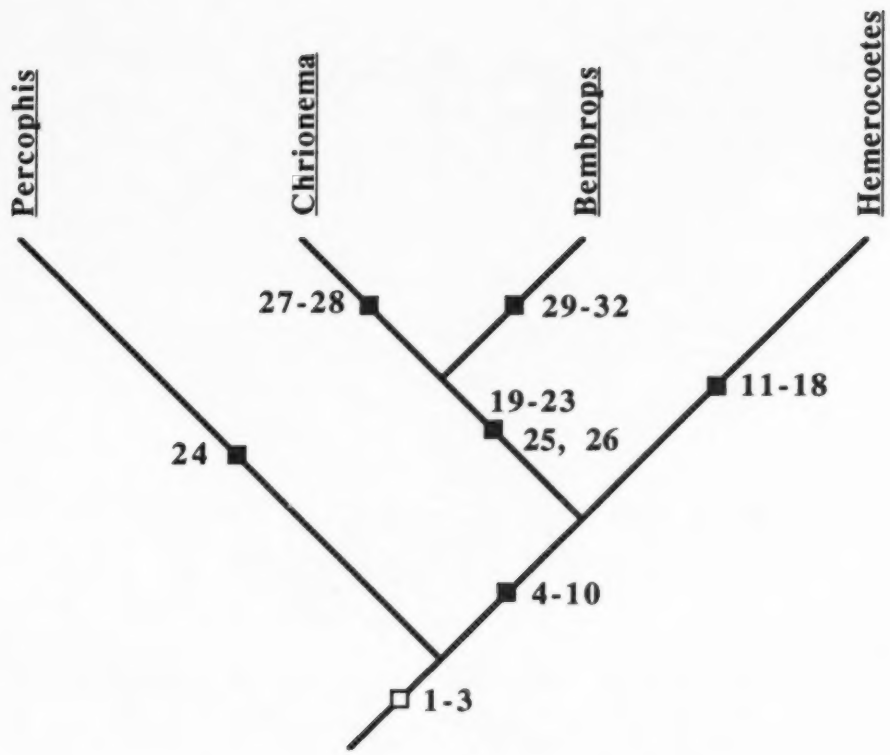


Fig. 6.1. Cladogram showing relationships of the four genera of the family Percophidae. Numerals refer to the characters described in the text. Characters indicated by closed squares are hypothesized as synapomorphies for each lineage. Hypothesized homoplasies are denoted by open square.

performed with the complete data set of 54 characters will be discussed in the section on interrelationship of the species of Bembrops.

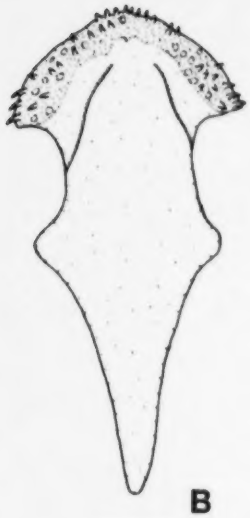
The four genera can be grouped together on the basis of three characters. The characters involve the hyomandibular bone [1], the pelvic girdle [2], and the mesopterygoid bone [3]. The hyomandibular has either a well-developed spur (Percophis) or an elevated crest (Bembrops, Chrionema and Hemerocoetes) on its lateral side, extending from the anterior edge to the area of the dorsal tip of the preopercle (character 3 in Pietsch, 1989). Pietsch (1989) observed hyomandibular spur in Percophis, but neither spur nor crest in other percophids. My examination of the osteological material suggests that Bembrops, Chrionema and Hemerocoetes do possess a hyomandibular crest. This character is also shared by other trachinoid families such as Pinguipedidae, Champsodontidae, Leptoscopidae, Trachinidae, and Uranoscopidae. The four genera share an anteroventrally directed spur on the pelvic bone. This character is also further shared by a number of other trachinoids such as, pinguipedids, trichonotids, creediids, champsodontids, chiasmodontids, cheimarrichthyids, leptoscopids, trachinids and uranoscopids (Pietsch, 1989). Nelson (1986) noted the morphological similarity of the mesopterygoid bone forming the floor of the orbit in creediids, trichonotids and Hemerocoetes. The other three percophid genera studied here also share this feature. All three characters, discussed above, are homoplasiously present among the four percophid genera I have studied, and I was unable to find any synapomorphy for the study group. A detailed phylogenetic study including all percophid genera would be needed to determine the monophyly of the family Percophidae.

Bembrops, Chrionema and Hemerocoetes form a monophyletic group on the basis of the following seven synapomorphies.

(1) Anterior head on vomer [4]. In Percophis, all of the anterior expanded head of vomer is covered with small teeth on its ventral surface (Fig. 6.2). The head of vomer

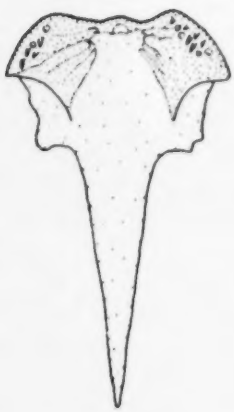
Fig. 6.2. Ventral view of the vomer in four percophid species showing character-state distribution for character 4 of the data matrix for the phylogenetic analysis. Horizontal bar equals 2 mm. A. Percophis brasiliensis, MZUSP 38920; B. Chrionema chlorotaenia, AMS I.22821-036; C. Bembrops curvatura, BSKU uncat.; D. Hemerocoetes pauciradiatus, VUW uncat.

A



B

C



D

shows a median groove in the other three genera, and as a result, teeth are restricted only on the ventrolateral edge of the head. Development of the medial groove and loss of teeth in the medial surface is considered the apomorphic state.

(2) Hyomandibular spur or crest [5]. A further apomorphic state of character 1. As was mentioned above, Percophis possesses a well developed lateral spur on the hyomandibular bone, whereas the other three genera are characterized by a lateral crest.

(3) Adult size [6]. Adult Percophis can reach a total length of more than 400 mm whereas the other three genera do not grow beyond 300 mm in total length.

(4) Skeleton [7]. In most part, the skeleton is thinner, lighter, and without much sculpturing as compared with Percophis.

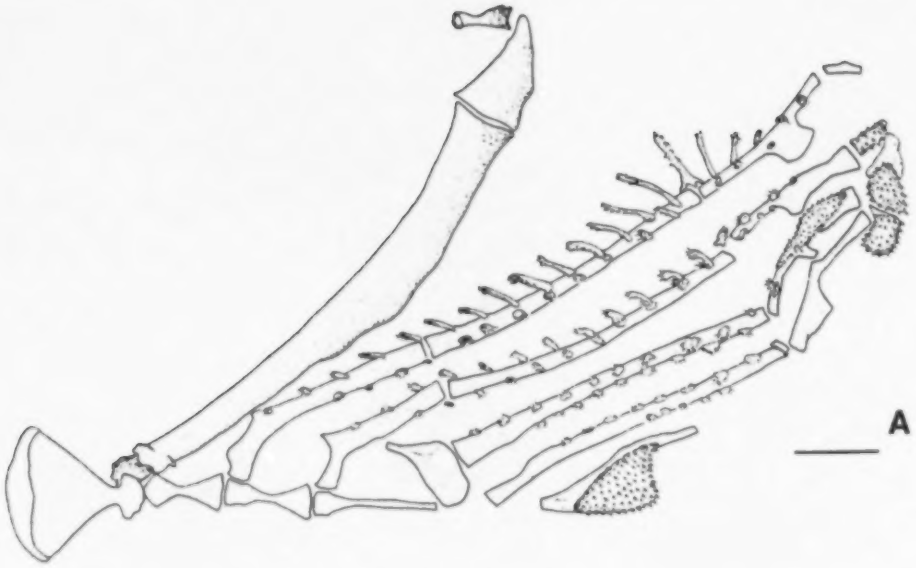
(5) Predorsal bone [8]. Percophis possesses five well-developed predorsal bones; the complete loss in other three genera is considered derived.

(6) Teeth on premaxillary symphysis [9]. There are 7 or 8 teeth in the symphysis area of the premaxilla of Percophis that are of extremely large in size compared to the other teeth. Although in Bembrops, Chrionema and Hemerocoetes, there is an increase in size of a number of teeth, the largest teeth are not as large as they are in Percophis. The reduced size is considered apomorphic for these three genera.

(7) Caudal fin rays [10]. Percophis has 13 principal caudal fin rays. Bembrops and Chrionema have 11 principal rays in their caudal fin, whereas Hemerocoetes has 10 rays. A reduction in number of principal rays is hypothesized as derived.

The clade consisting of Bembrops and Chrionema is supported by seven synapomorphies: (1) somewhat goblet-shaped nasal bone with a distinct passage for the supraorbital canal [19]; (2) sixth branchiostegal ray either attached to the ceratohyal bone or situated at the junction of the ceratohyal and epihyal [20] (Fig. 6.3), whereas Percophis (Fig. 6.4) and Hemerocoetes the have last two branchiostegal rays attached to the epihyal; (3) scales mostly ctenoid or reduced ctenoid [21] in Bembrops and Chrionema, whereas

Fig. 6.3. The branchial apparatus and the hyoid apparatus of Bembrops filifera, ex-BPBM 24273, showing character-state distribution for character 20, 32, 50 and 54 of the data matrix for the phylogenetic analysis: A. Dorsal view of the right side; branchiostegal rays, and cartilages (except basihyal cartilage) not shown. Horizontal bar equals 5 mm. B. Left lateral view. Horizontal bar equals 5 mm.


A

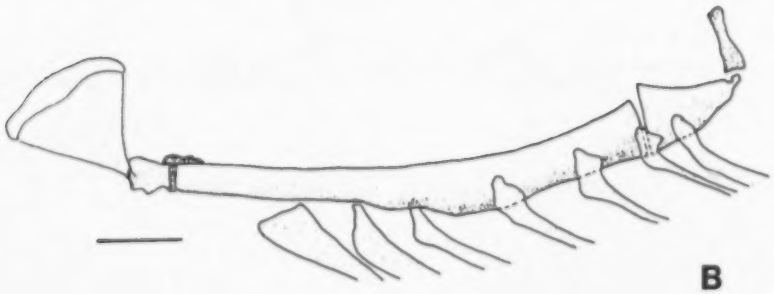
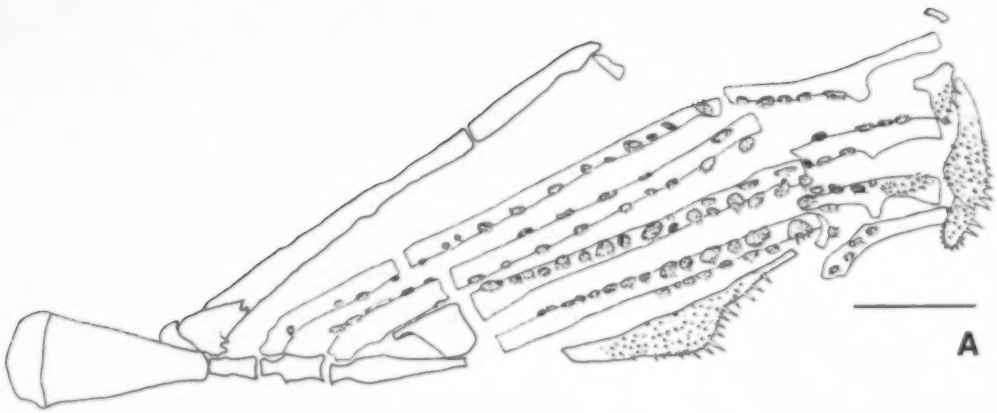
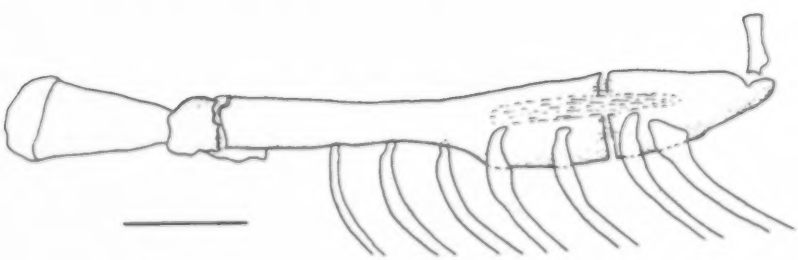

B

Fig. 6.4. The branchial apparatus and the hyoid apparatus of Percophis brasiliensis. MZUSP 38920, showing character-state distribution for character 20, 32, 50 and 54 of the data matrix for the phylogenetic analysis: A. Dorsal view of the right side; branchiostegal rays, and cartilages (except basihyal cartilage) not shown. Horizontal bar equals 5 mm.; B. Left lateral view. Horizontal bar equals 5 mm.



A



B

Percophis and Hemerocoetes have cycloid scales, the plesiomorphic state; (4) two opercular spines [22] compared to one found in Percophis and Hemerocoetes; (5) presence of preopercular spine [23]; (6) a distinct gap on the ventral region of the orbit between the lacrymal and the second infraorbital bone [25], whereas the infraorbital bones are connected to each other in Percophis and Hemerocoetes; (7) number of vertebrae [26] 27 or 28 in Bembrops and Chrionema, whereas it is more than 40 in the other two genera.

Four synapomorphies support the monophyly of all members of the genus Bembrops. All species of Bembrops possess a well-developed tentacle at the posterior tip of the maxilla [29]. The maxillary tentacle is absent in Percophis, Chrionema and Hemerocoetes. However, a barbel is present at the tip of the upper jaw in mature males of H. monopterygius (Nelson, 1979). I have considered the presence of a tentacle in Bembrops as a derived state. The posterior tip of the maxilla shows a deep notch (where the tentacle attaches) in all species of Bembrops [30]. The notch is very shallow in the other three genera. The third synapomorphy is associated with the palatine bone and its connection with the mesopterygoid [31] (Fig. 6.5). In Percophis, Chrionema and Hemerocoetes, the palatine develops a distinct bony plate-like connection between its two posteriorly directed components, and the mesopterygoid is broadly connected to this region. In Bembrops, this medial bony connection is indistinct, and as a result, there is a distinct median gap anteriorly where the mesopterygoid is attached to the components of the palatine. The third branchiostegal ray in Bembrops widens proximally where it attaches to the ceratohyal [32] (Fig. 6.3). It is very narrow and slender along its entire length in other genera.

Percophis is a monotypic genus distinctive among the four genera in having a modified urohyal bone consisting of five posteriorly elongated prongs [24] (Fig. 6.6). It also shares the apomorphic states of counts of dorsal and ventral procurrent rays [27, 28] with Bembrops (Fig. 6.7).

Fig. 6.5. Ventral view of the palatine, ectopterygoid and mesopterygoid showing character-state distribution for character 31 and 52 of the data matrix for the phylogenetic analysis: A. Chrionema chlorotaenia, AMS I.22821-036; B. Bembrops anatirostris, UF 20747. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.

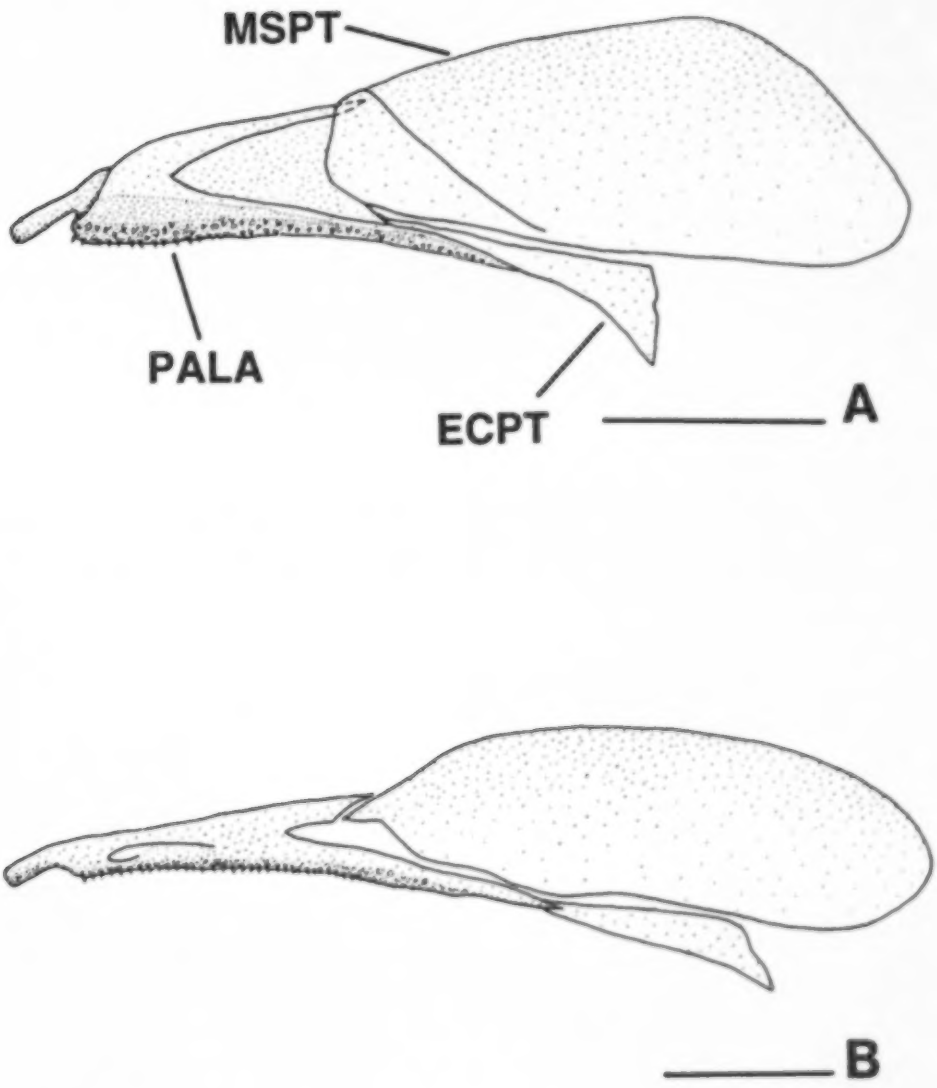
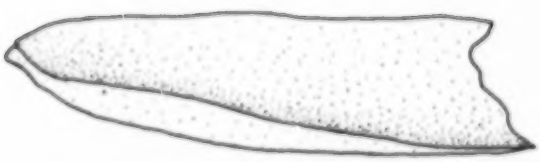

MSPT
PALA
ECPT
A
B

Fig. 6.6. Left lateral view of the urohyal showing character-state distribution for character 24 and 53 of the data matrix for the phylogenetic analysis: A. Percophis brasiliensis, MZUSP 38920; B. Chrionema chlorotaenia, AMS I.22821-036; C. Hemerocoetes pauciradiatus, VUW uncat.; D. Bembrops anatirostris, UF 20747; E. B. macromma, UF 47052. Horizontal bar equals 3 mm.

A

B

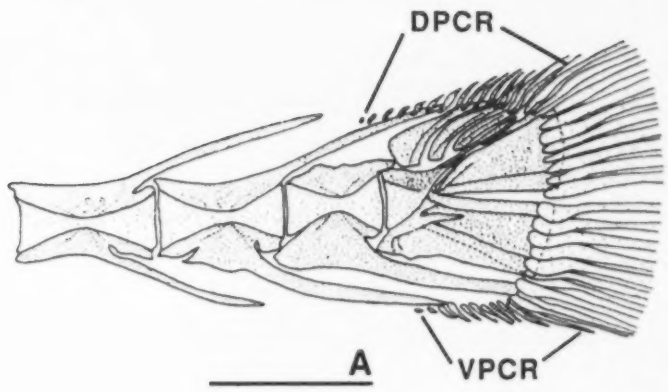
C

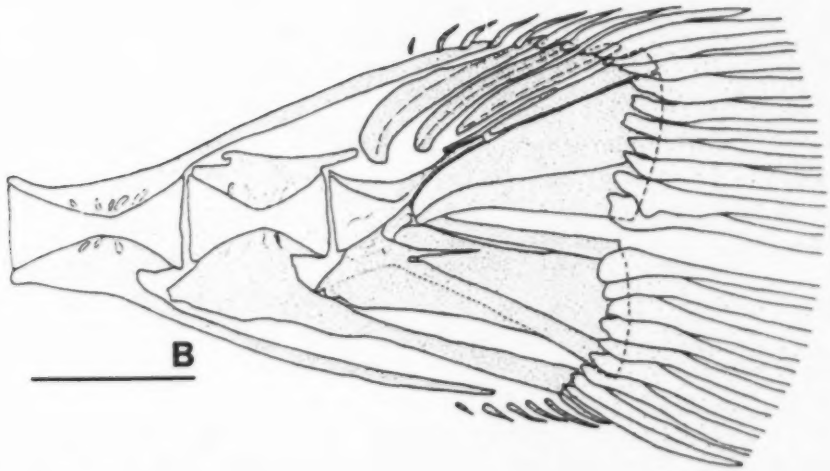


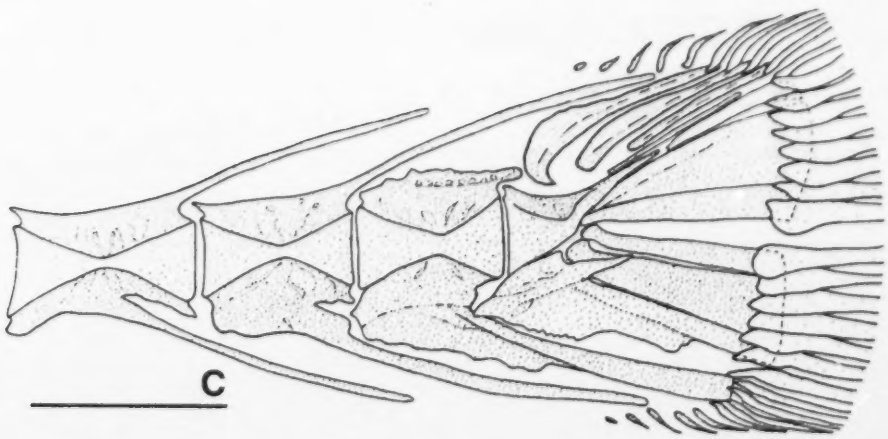
D

E

Fig. 6.7. Left lateral view of the caudal skeleton showing character-state distribution for character 27, 28 and 42 of the data matrix for the phylogenetic analysis: A. Chrionema chlorotaenia, AMS I.22821-036; B. Bembrops gobioides, UF 40089; C. B. heterurus, UAMZ 4647. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


DPCR
VPCR
A


B


C

The two synapomorphies shared by the species of Chrionema are the dorsal and ventral procurrent rays [27, 28] being maximum in counts (Fig. 6.7).

Hemerocoetes is the most derived among the four genera studied in this analysis. The synapomorphies supporting this view are: 1) exposed spine on the anterior tip of maxilla [11]; 2) long ascending process of premaxilla [12]; 3) absence of spinous dorsal fin [13]; 4) absence of teeth on palatine bone [14]; 5) flat epurals [15]; 6) hypural bones fused together to form a dorsal and a ventral hypural plate [16]; 7) absence of anterior and posterior process on the pelvic girdle [17]; 8) scapula and coracoid not extended up to the posterolateral margin of cleithrum [18]. The mesopterygoid in this species is also slightly curved upward but does not reach the neurocranium.

INTERRELATIONSHIPS OF SPECIES OF BEMBROPS

The following section discusses the phylogenetic interrelationships of 13 species of the genus Bembrops. Because of little variation in morphological characters among different species, relatively few characters were available for use in the phylogenetic analysis. Osteological materials were not available for six species. It was possible to examine certain osteological characters (mostly restricted to the caudal skeleton) using x-rays for those species. For nine osteological characters (characters 46-54), however, data were entered as missing values in the data matrix. PAUP deals with missing data by assigning a character state "that would be most parsimonious given its placement on the tree" (Swofford, 1991). The phylogenetic interrelationships proposed herein should be considered a working hypothesis of the interspecific relationships.

As mentioned before, the analysis was done in two phases where the data matrix of 54 characters (Table 3.1, Appendix IV) was run using both heuristic and branch-and-bound search options. The heuristic search (branch swapping, NNI option) produced only

one parsimonious cladogram with a length of 84 steps and consistency index of 0.643 (Fig. 6.8). The branch-and-bound search resulted in 23 equally minimal-length cladograms with a length of 83 steps and consistency index of 0.651. The branch-and-bound method was helpful in finding 22 extra minimal-length cladograms, with a single step difference in length of cladograms between the two methods. Strict, semistrict, and Adams consensus cladograms were generated from the 23 cladograms of the branch-and-bound run, and they show a polychotomy involving most species of Bembrops. Consensus cladograms are usually produced by recognizing only the unequivocal components in the data (Anderberg and Tehler, 1990), i.e., by retaining only those components that are present in all parsimonious cladograms. Miyamoto (1985) argued that parsimonious resolutions of the original data are not represented in the consensus cladograms because "consensus cladograms are generated from fundamental cladograms instead of original information." Mickevich and Farris (1981) also supported Miyamoto's view. Controversy also exists regarding the use of consensus cladograms in classification because they have less resolution than any of the parsimonious cladograms from which they are calculated (Carpenter, 1988). Wiley et al. (1991) also suggested against using a consensus tree "as a phylogeny unless it is topologically identical with one or more of the most parsimonious trees".

Due to poor resolution of the consensus cladograms (Fig. 6.9 shows the strict consensus cladogram with nine lineages forming a polychotomy), the final classification was produced from one of the 23 parsimonious cladograms generated by the branch-and-bound method. I have selected the cladogram that is characterized by the minimum amount of ambiguity (Figs. 6.10 and 6.11). Although many of the characters used in this analysis are homoplasiously distributed in the cladogram, the cladogram clearly shows how the characters are distributed among the taxa. The distribution can also be tested in the future by adding additional characters to the cladogram. Five nodes are recognized in the

Fig. 6.8. Cladogram for the relationships of 13 species of Bembrops and the members of the outgroup produced by the heuristic method of PAUP based on a data matrix of 54 characters. Length of the cladogram is 84 and consistency index is 0.643. Asterisks refer to the species with data collected for all 54 characters.

Fig. 6.9. Strict consensus cladogram of 13 species of Bembrops and the members of the outgroup produced by the branch and bound method of PAUP based on a data matrix of 54 characters. Length of the cladogram is 83 steps and consistency index is 0.651.

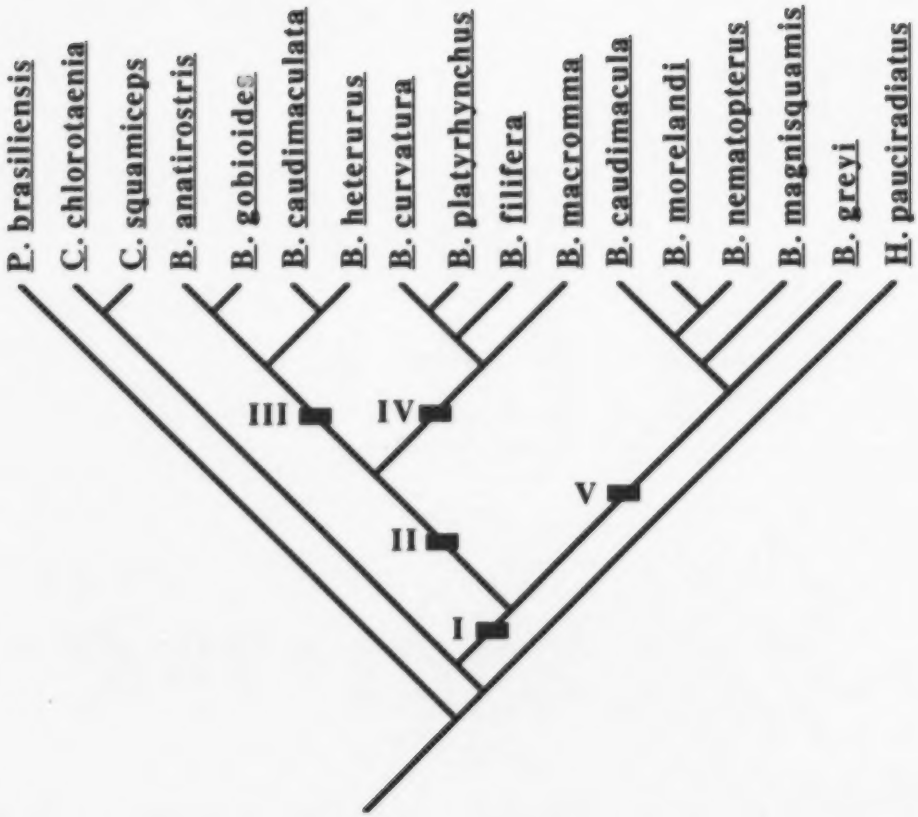


Fig. 6.10. Cladogram for the relationships of 13 species of Bembrops and the members of the outgroup. Roman numerals indicate nodes. See text for discussion.

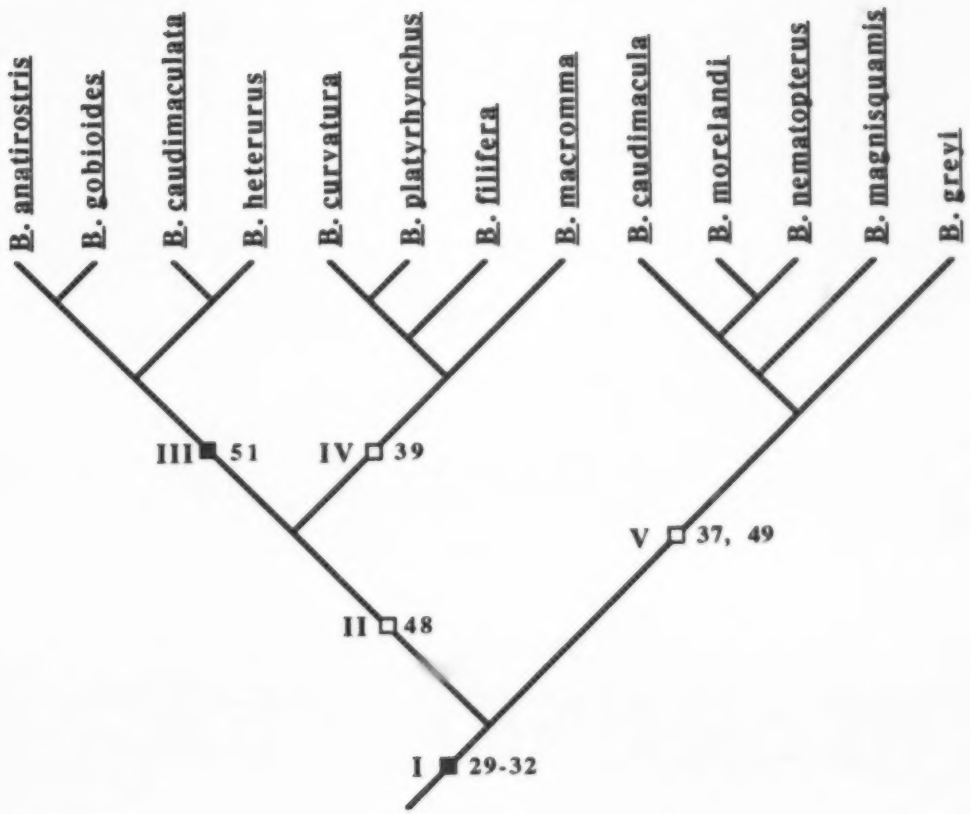


Fig. 6.11. Cladogram for the relationships of 13 species of Bembrops showing distribution of characters for five nodes. Roman numerals indicate nodes and numerals refer to the characters described in the text. See text for discussion. Characters indicated by open squares are homoplastic states. Characters indicated by closeed squares are hypothesized as synapomorphies for each lineage. Hypothesized homoplasies are denoted by open squares.

cladogram beginning with the node where all species of Bembrops are connected in the tree as being node I. Character distribution of this node is discussed in the previous section on the monophyly of the genus.

Another data set was selected from the original data matrix where six species of Bembrops having no information for characters 46-54 were excluded from the analysis. Both the heuristic and the branch-and-bound methods produced a single minimal length cladogram with a length of 75 steps and consistency index of 0.72 (Fig. 6.12). The interrelationships among the seven species remain identical as it was in the analysis with all 13 species.

NODE II GROUP (Figs. 6.10 and 6.11)

This node includes eight out of 13 species of Bembrops. One synapomorphy defines this group: pointed dorsal margin of metapterygoid [48] (Fig. 6.13). Members of this group share this apomorphic state with H. pauciradiatus. The other three members of the outgroup (Percophis brasiliensis, Chrionema chlorotaenia and C. squamiceps) have a flat dorsal margin which is considered as the primitive state.

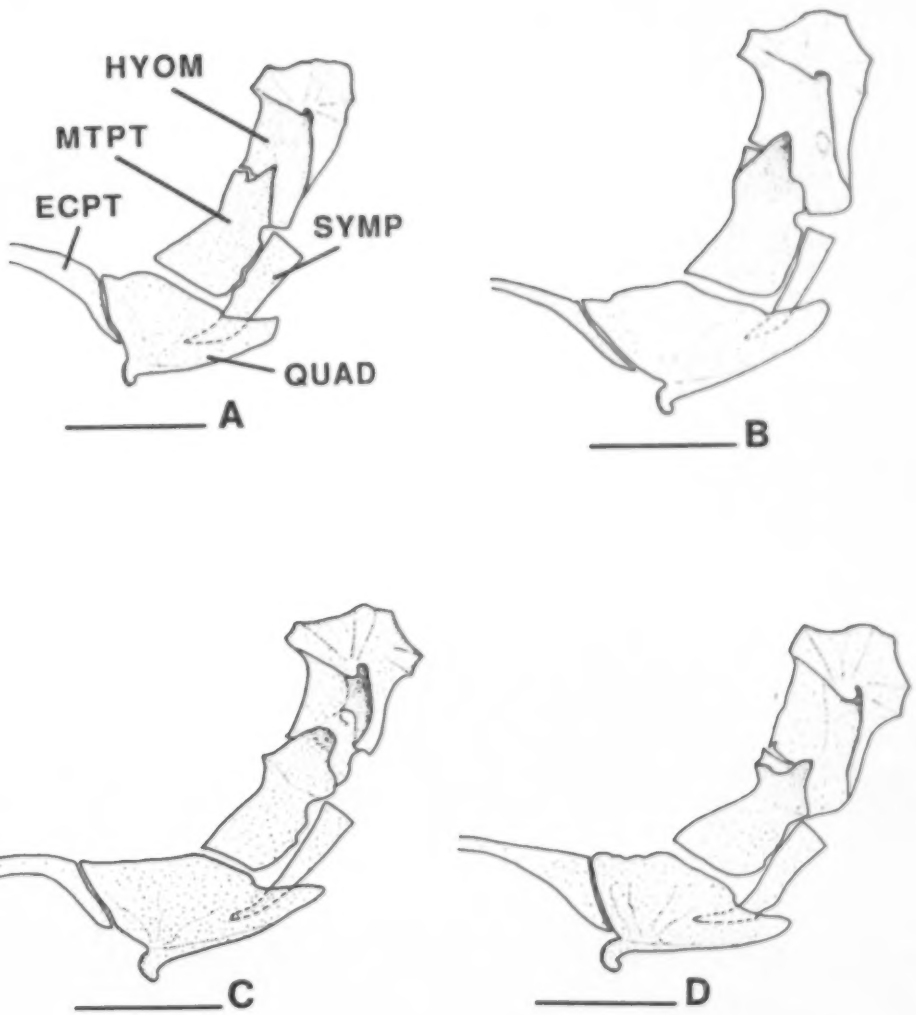
NODE III GROUP (Figs. 6.10, 6.11 and 6.14)

This node comprises four species – B. anatirostris, B. gobioides, B. caudimaculata and B. heterurus. These four species share a single synapomorphy which is unique to this node: anterior end of the third hypobranchial not extended [51] (Fig. 6.15).

Within this node, a sister-group relationship between B. anatirostris and B. gobioides is supported by three derived states: 1) presence of a tiny spine-like extension at the posterodorsal tip of interopercle [44]; 2) short anterior process of pelvic bone [46]

Fig. 6.12. Cladogram for the relationships of seven species of Bembrops and the members of the outgroup for which data was available for all 54 characters. Both heuristic and branch and bound methods of PAUP produced a single cladogram with a length of 75 steps and a consistency index of 0.72.

Fig. 6.13. Left lateral view of the suspensorium showing character-state distribution for character 47, 48 and 49 of the data matrix for the phylogenetic analysis: A. Bembrops curvatura, BSKU uncat.; B. B. gobioides, UF 40089; C. B. filifera, ex-BPBM 24273; D. B. platyrhynchus, AMS I.20118-019. Mesopterygoid, palatine, and anterior part of ectopterygoid not shown. Horizontal bar equals 5 mm. See Appendix III for the list of abbreviations for identification of osteological structures.


HYOM
MTPT
ECPT
SYMP
QUAD
A
B
C
D

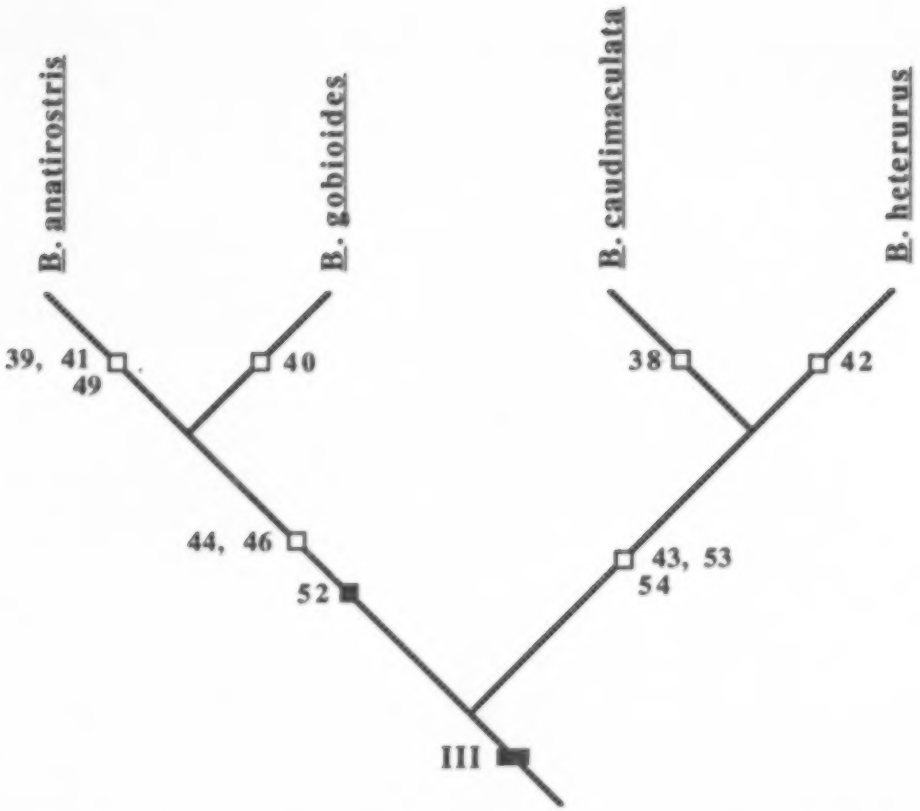
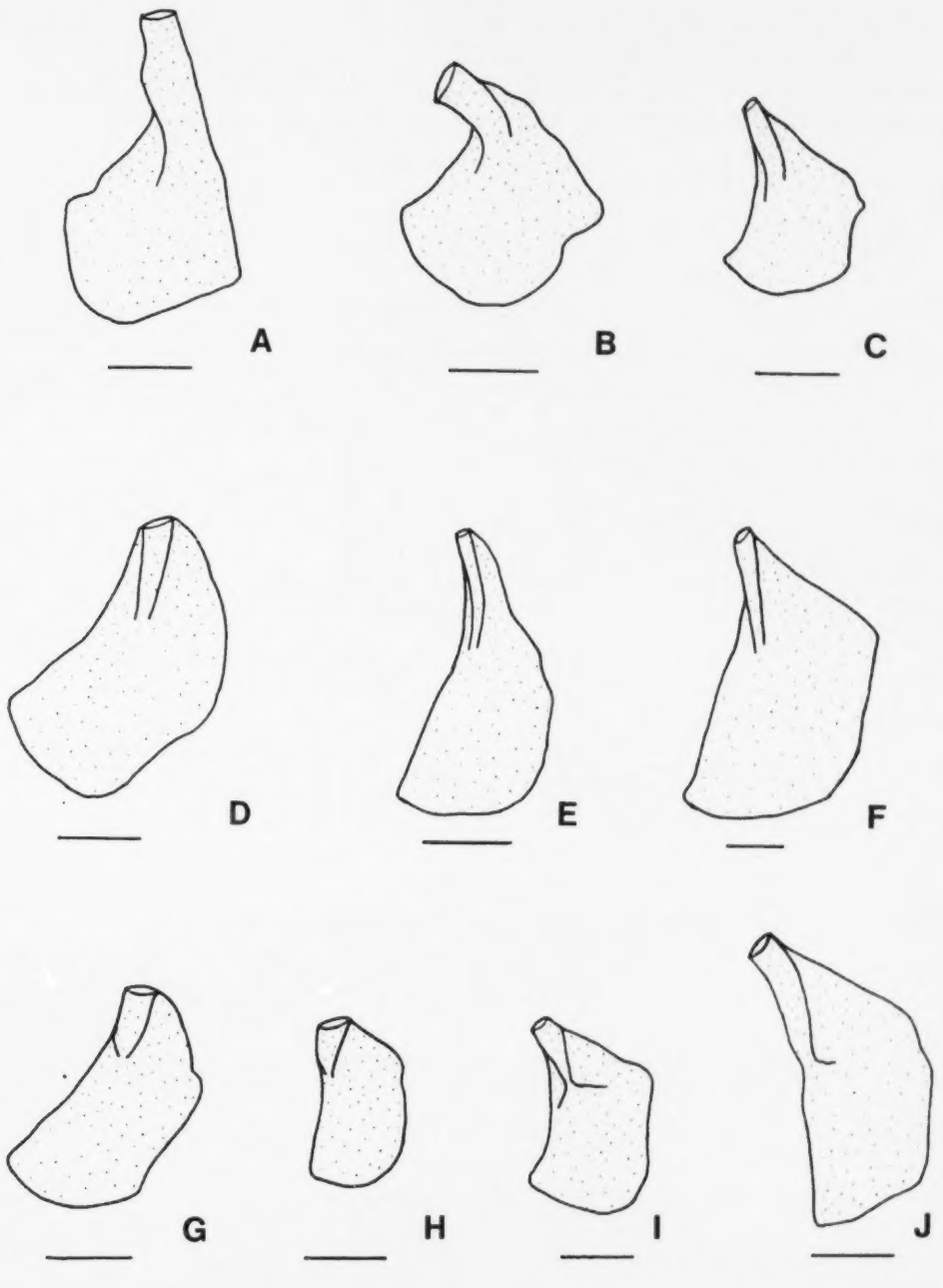


Fig. 6.14. Cladogram showing character support for four species of Bembrops at node III of the original cladogram (Fig. 6.11). Numerals refer to the characters described in the text. Character indicated by closed square is hypothesized as synapomorphy for the lineage. Hypothesized homoplasies are denoted by open squares.

Fig. 6.15. Dorsal view of the third hypobranchial of right side showing character-state distribution for character 51 of the data matrix for the phylogenetic analysis: A. Percophis brasiliensis, MZUSP 38920; B. Chrionema chlorotaenia, AMS I.22821-036; C. C. squamiceps, ex-BPBM 23866; D. Bembrops anatirostris, UF 20747; E. B. curvatura, BSKU uncat.; F. B. filifera, ex-BPBM 24273; G. B. gobioides, UF 40089; H. B. heterurus, UAMZ 4647; I. B. macromma, UF 47052; J. B. platyrhynchus, AMS I.20118-019. Horizontal bar equals 1 mm.


A
B
C
D
E
F
G
H
I
J

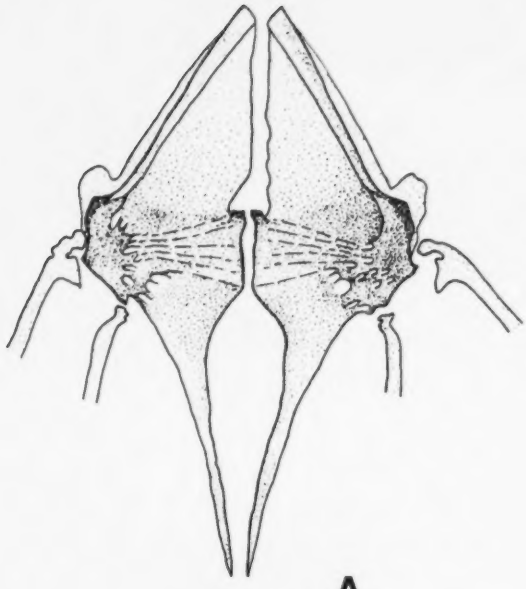
(Fig. 6.16) and 3) only one or two rows of fine teeth at the anterior end of palatine with rows increasing toward posterior end [52] (Fig. 6.5). Character 44 is also shared by B. macromma. Pelvic with short anterior process is also seen in C. chlorotaenia. Character 52 is a synapomorphy not shared by any other species. B. anatirostris also shares three other homoplasies: elongation of anterior spines of first dorsal fin [39]; longer snout length [41] and absence of a small fossa in hyomandibular at its posterolateral margin [49] (Fig. 6.13). B. gobioides shares abruptly descending lateral line [40] with B. curvatura.

The other two species of the node III group also are sisters and share three homoplasies, two of which are apomorphic states: extended posteromedian margin of urohyal [53] (Fig. 6.6) and absence of a notch at the posterodorsal end of epihyal [54]. Character state 53 is shared by B. macromma and character state 54 is shared by B. curvatura and B. platyrhynchus. A reversal is also present in this clade: hypural 1 and 2 not attached to each other.

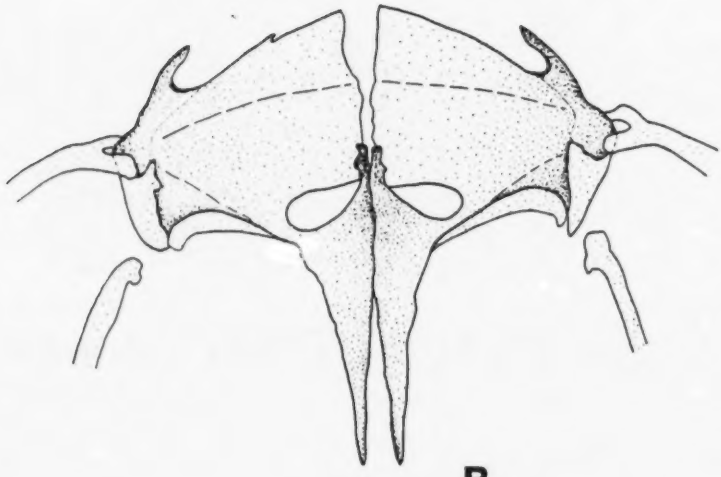
NODE IV GROUP (Figs. 6.10, 6.11 and 6.17)

The node IV group contains four species and is supported by one homoplastic character state: elongation of anterior spines of first dorsal fin [39]. B. anatirostris from node III group and C. squamiceps also share this derived state. B. curvatura, B. platyrhynchus and B. filifera form a clade by the presence of single unique derived character: short basihyal with anterior margin wider [50]. The basihyal is more or less triangular in shape in both the outgroups and the ingroup, and shows two states – elongated and narrower anteriorly, and shorter, wider anteriorly (Figs. 6.3 and 6.4). The elongated basihyal is characteristic for members of the outgroup hence the elongate state is considered as the primitive state. Pietsch (1989) considered this state as characteristic for

Fig. 6.16. Ventral view of the pelvic girdle showing character-state distribution for character 45 and 46 of the data matrix for the phylogenetic analysis: A. Percophis brasiliensis, MZUSP 38920; B. Bembrops filifera, ex-BPBM 24273. Horizontal bar equals 5 mm.



A



B

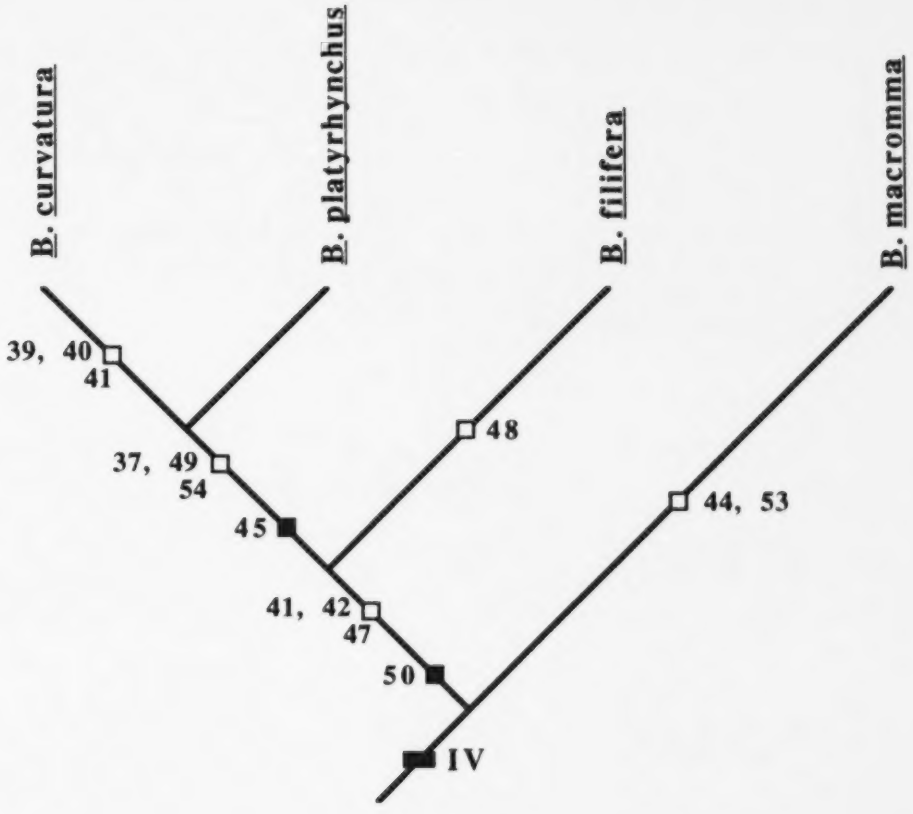


Fig. 6.17. Cladogram showing character support for four species of Bembrops at node IV of the original cladogram (Fig. 6.11). Numerals refer to the characters described in the text.Characters indicated by closeed squares are hypothesized as synapomorphies for each lineage. Hypothesized homoplasies are denoted by open squares.

the family Percophidae. My study shows variation in this character among the members of Bembrops.

This clade also shares three other homoplastic states : 1) longer snout length [41]; 2) pointed epural 1 [42] (Fig. 6.7); and 3) relatively long symplectic [47] (Fig. 6.13). B. curvatura shows a further reversal of character 41 by possessing a shorter snout length.

Length of symplectic was established by examining the termination of its dorsal margin compared to the posterior notch of the metapterygoid. In the outgroup (except H. pauciradiatus) the symplectic does not reach the dorsal margin of the notch, and hence is considered shorter.

The sister-group relationship between B. curvatura and B. platyrhynchus is supported by one synapomorphic state: relatively short posterior process of pelvic bone [45] (Fig. 6.16). Three homoplasies can also be recognized: 1) lateral-line scales less than 60 [37]; 2) absence of a small fossa in hyomandibular at its posterolateral margin [49] and 3) absence of notch at the posterodorsal end of epihyal [54]. These three homoplastic states are hypothesized to be a result of evolutionary convergence.

NODE V GROUP (Figs. 6.10, 6.11 and 6.18)

The node V group comprises five species and is supported by two synapomorphies: 1) lateral-line scales less than 60 [37] and 2) absence of a small fossa in hyomandibular at its posterolateral margin [49]. Both these states are also shared by B. curvatura and B. platyrhynchus. A reversal in peritoneum color [38] characterizes a clade comprising B. caudimacula, B. morelandi, B. nematopterus and B. magnisquamis. A sister-group relationship between B. caudimacula, and B. morelandi and B. nematopterus is supported by longer snout length [41]. B. morelandi and B. nematopterus form a clade and their

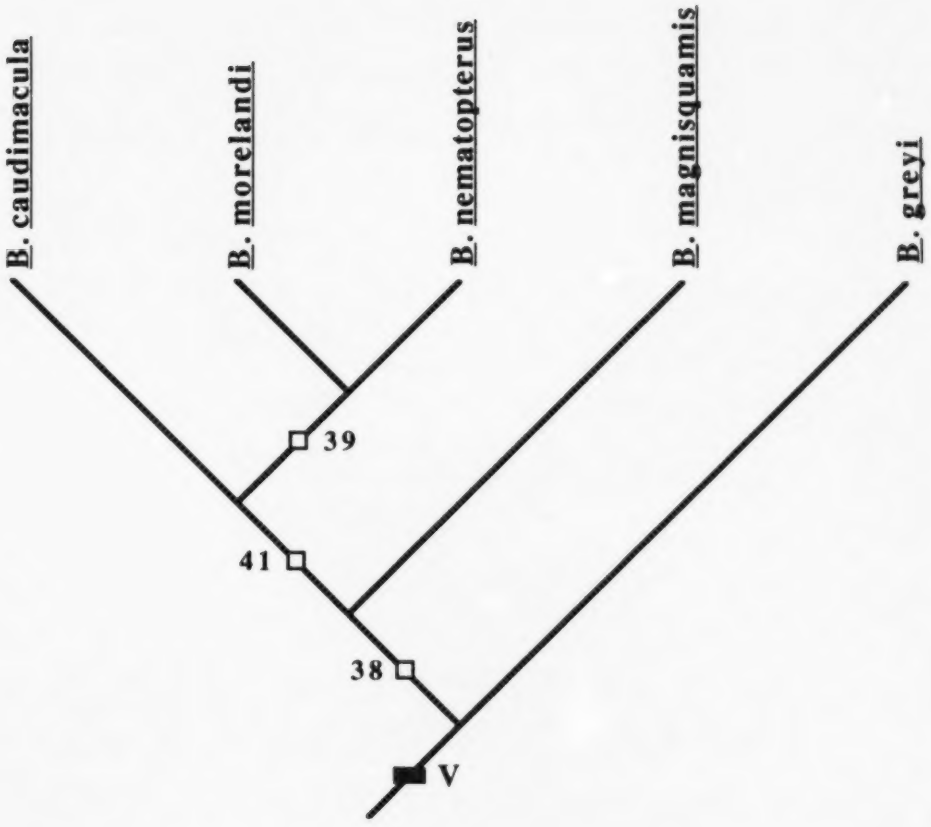


Fig. 6.18. Cladogram showing character support for five species of Bembrops at node V of the original cladogram (Fig. 6.11). Numerals refer to the characters described in the text. Characters indicated by open squares are homoplastic states.

sister-group relationship is supported by one apomorphic state – elongation of anterior spines of first dorsal fin. The two species are also characterized by the primitive state for the number of gill rakers on the lower limb of gill arch.

7. BIOGEOGRAPHY

Bembrops has an Indo-West Pacific and Atlantic distribution and inhabits the continental shelf and slope areas between depths of 50 and 700 m (Figs. 4.2, 4.7, 4.9 and 4.12). The distributional information presented in these figures is based on information compiled from various sources, including the materials examined, the original descriptions of the species, and other literature sources. In this section I will discuss the biogeography of Bembrops after briefly discussing three possible approaches to such a study, track analysis, vicariance, and dispersal. A detailed biogeographic analysis is not intended here; rather a basis for distributional data and biogeographic hypotheses is presented for analyses of related taxa in future studies.

Most workers think it necessary to consider vicariance and dispersal events to study the biogeography of a taxon. However, there are differences of opinion about the relative importance of dispersal versus vicariant events in explaining biogeographic patterns. According to vicariance biogeography, distributions of taxa are generally explained by fragmentation of previous continuous distributions, a process by which the range of a group is split by a vicariant event (climatological, geological, etc.). Allopatric speciation may result from such fragmented ranges. It is acknowledged by many vicariance biogeographers that dispersal events are supported when relatively closely related species occur in sympatry, but that otherwise one should attempt to explain biogeographic patterns by looking for congruence between vicariant events and phylogenetic events. In this section I will deal with both the above approaches to biogeography, including Croizat's track analysis which proposes that similarities in distribution among various taxa can lead us to the recognition of a general distributional pattern.

TRACK ANALYSIS

If the area cladograms of various unrelated taxa show any congruence, a general distributional pattern, a generalized track, can be supported. Once recognized, these tracks can then be used to search for geological or vicariance events to explain the observed distributional patterns. A simple interpretation could be that congruence would imply shared history, incongruence independent dispersals. The following four generalized tracks are predicted in terms of the distributional patterns of the species of Bembrops (Fig. 7.1) and they are compared with some already established hypotheses.

1) tropical and warm temperate Indo-West Pacific and Atlantic – the family Percophidae;

2) western Atlantic (including Gulf of Mexico and Caribbean)-eastern Atlantic – species of node III group;

3) Gulf of Mexico-Caribbean-Indian Ocean-Indo-West Pacific (including Hawaii) – species of node IV group;

4) Caribbean-Eastern Atlantic-Indo-West Pacific (including New Zealand) – species of node V group.

The present distribution of the family Percophidae describes a generalized track consisting of tropical and warm temperate continental shelf and slope areas of the Atlantic and Indo-West Pacific. The eastern Pacific-eastern Atlantic track is considered to be the oldest transoceanic generalized track in this region of the world (Rosen, 1976). The distribution of percophids is not relevant to this track because of the total absence of the family in the eastern Pacific. A detailed phylogenetic study including all percophid genera is needed to search for other tracks within the family.

Springer (1982), in his study of the Indo-Pacific shorefishes, pointed out that there are few cladistic studies of Indo-Pacific organisms. Likewise, there is very little

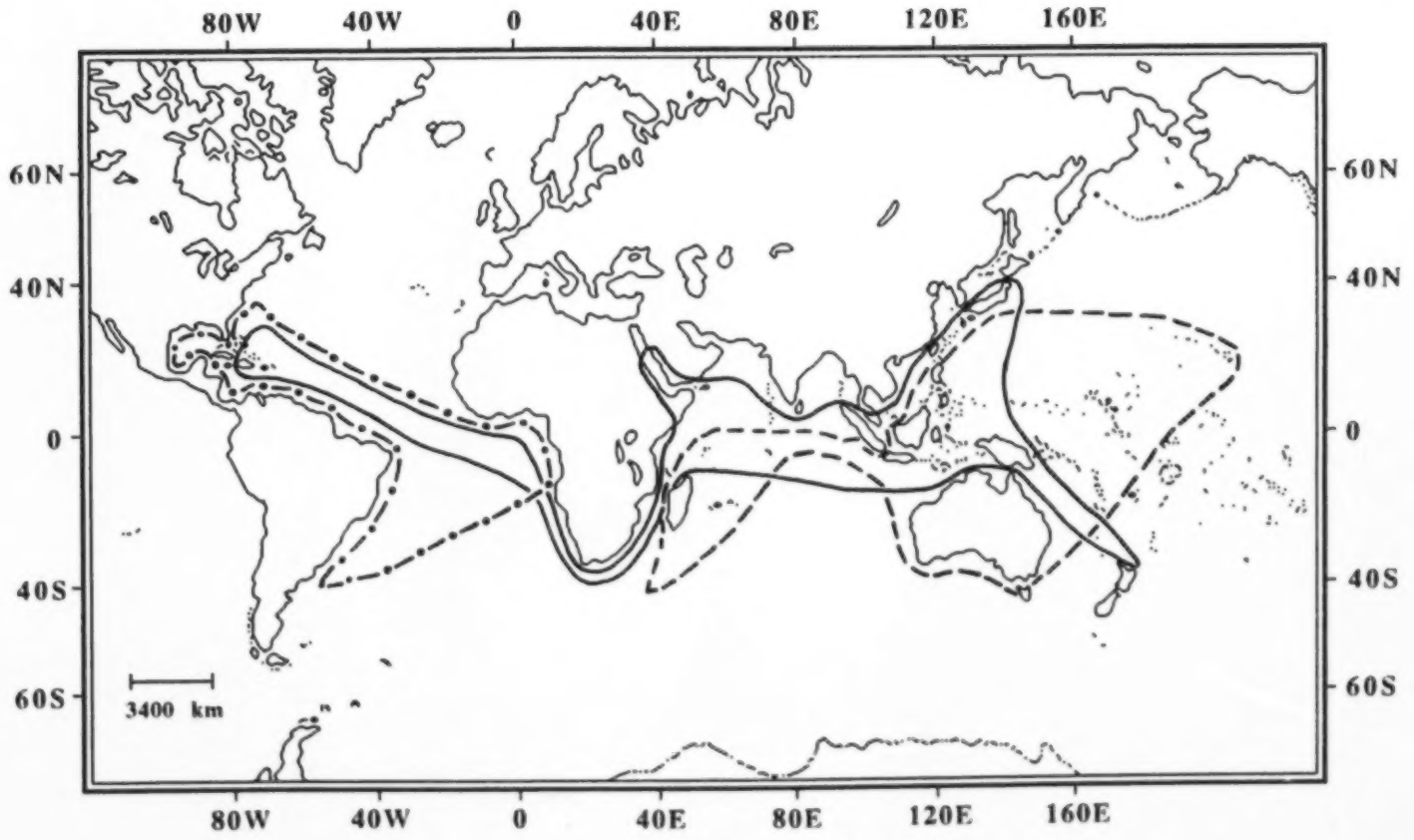


Fig. 7.1. Generalized distribution tracks of node III (-·-), IV (- -) and V (—) species groups of Bembrops (see Fig. 6.11) based on the available distribution data.

information for Atlantic taxa (Howes, 1991). As mentioned before, there are also few cladistic studies of most members of the suborder Trachinoidei. Therefore, I have relied on the relationships of the 13 species of Bembrops based on the final cladogram (Fig. 6.11), to make their area cladogram (Fig. 7.2). The phylogeny of the species has been replaced by their respective geographic distributions and as a result, instead of implying simple relationships among different species, they now also represent relationships among areas. To expedite comparison between species groups, the nodes of the area cladogram are numbered in the same order as the nodes of the phylogenetic cladogram.

VICARIANCE BIOGEOGRAPHY

A number of methodologies have been developed during the recent past to construct area cladograms based on information gathered from the phylogeny (see Mayden, 1988 for a brief discussion of these methods). I have used Brooks' Parsimony Analysis to construct the area cladogram representing the distributional patterns of the species of Bembrops.

Brooks (1981, 1988, 1990) developed a parsimony analysis (Brooks' Parsimony Analysis) to study the geographical distribution of taxa based on phylogenetic relationships. According to this method, "each taxon and each internal branch in the cladogram is numbered." Each species is given a code to indicate its identity and its common ancestry. Later, these codes are replaced by a set of binary codes (0's and 1's) in the data matrix, where the presence of a number in a species or its ancestor is identified as "1" and its absence as "0". Finally, the species names are replaced by the geographic areas of their occurrence. When a species is absent in a particular area, it is treated as a missing datum. The binary data matrix can then be run using PAUP, and cladogram(s) generated by the program would represent the area relationship. The distributional data and the

Fig. 7.2. Area cladogram for the 13 species of Bembrops based on distribution data. Roman numerals indicate nodes presented in Fig. 6.11. See text for discussion.

phylogenetic relationships of 13 species of Bembrops were used to develop a data matrix (Table 7.1) that was then run in PAUP, and the result is presented in the form of an area cladogram.

A strict consensus area cladogram is presented in Fig. 7.3 based on the phylogenetic relationships of 13 species of Bembrops following methods of Brooks' Parsimony Analysis. The consensus cladogram was calculated from 4 equally minimal-length trees with a length of 62 steps and consistency index of 0.823 and produced by the branch-and-bound method of PAUP 3.0s.

The four regions of the Atlantic form a trichotomy in the strict consensus cladogram and two of the four minimal-length cladograms. In the other two minimal-length cladograms, southwestern Atlantic and eastern Atlantic form a monophyletic group. The Atlantic clade is characterized by three homoplasies. Presence of B. macromma of node IV species group and B. magnisquamis of node V species group can be considered as reversals. According to the vicariance model, this can be attributed to subsequent extinction of these species. Presence of B. caudimacula in the eastern Atlantic is a parallelism which demonstrates a dispersal event.

The Indo-West Pacific clade also comprises an unresolved polychotomy among its five areas. Indian Ocean, Indo-Malay and Japan are classified together in a polychotomy, and southern Australia-New Zealand and Hawaii form another clade. In this analysis, two species, B. platyrhynchus of node IV and B. caudimacula of node V, are present in multiple areas because of their widespread distributional patterns. As mentioned above, B. caudimacula also homoplasiously occurs in the previous clade. These two species suggest strong evidence for dispersal within different regions of the Indo-West Pacific and also between the western Indian Ocean and the eastern Pacific.

Table 7.1. Data matrix for nine distributional regions and binary codes for 13 species of Bembrops based on the phylogeny presented in Chapter 6. '?' indicates missing taxa.

```
[ 1-5  6-10  11-15 16-20 21-25 26-30 31-35 36-40 41-45 46-50 51-55 56-60 61-65 66-70 71-75 76-80 81-85 86-90 91-95 96-100]
[12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890 12345 67890]

Gulf of Mexico
 10000 00000 00010 00000 10101 01000 00000 00010 00000 10101 00000 00100 00000 00000 01101 ????? ????? ????? ????? ?????

Caribbean
 10000 00000 00010 00000 10101 01000 00000 00010 00000 10101 00000 00000 01000 00001 00011 00000 00100 00000 00000 01101

Southwestern Atlantic
 00010 00000 00001 00000 10101 ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????

Eastern Atlantic
 00100 00000 00001 00000 10101 00010 00000 00001 00000 10101 00000 00010 00000 00011 00011 00000 00000 00100 00000 00011

Indian Ocean
 00000 00010 00000 00011 00011 00000 00000 10000 00111 00011 00000 10000 00000 11000 01101 ????? ????? ????? ????? ?????

Indo-Malay
 00000 00010 00000 00011 00011 00001 00000 00000 11000 01101 00000 10000 00000 11000 01101 00000 01000 00000 01000 01101

Southern Australia and New Zealand
 00000 10000 00000 11000 01101 00000 00001 00000 00111 00011 ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????

Japan
 00000 00010 00000 00011 00011 00001 00000 00000 11000 01101 00000 01000 00000 01000 01101 ????? ????? ????? ????? ?????

Hawaii
 00000 01000 00000 01000 01101 ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
```

Fig. 7.3. Strict consensus area cladogram for the 13 species of Bembrops based on their phylogenetic relationships (Fig. 6.11) using Brooks' Parsimony Analysis. The consensus cladogram was produced from four equally minimum-length trees generated by the branch-and-bound method of PAUP. Treelength = 62; consistency index = 0.823. Numbers refer to 13 species of Bembrops. 1 = B. anatirostris; 2 = B. gobioides; 3 = B. caudimaculata; 4 = B. heterurus; 5 = B. curvatura; 6 = B. platyrhynchus; 7 = B. filifera; 8 = B. macromma; 9 = B. caudimacula; 10 = B. morelandi; 11 = B. nematopterus; 12 = B. magnisquamis; 13 = B. greyi.

DISPERSAL BIOGEOGRAPHY

Dispersal biogeography explains the distributional patterns of any taxon in terms of actual movement of individuals, either actively or passively, to new areas. The recognition of biogeographic regions, an important part of the dispersal approach to biogeography, is based on the degree of endemism of organisms (Ekman, 1953; Briggs, 1987). I accept the traditional regional divisions except that within the Atlantic region, I have recognized the Gulf of Mexico and Caribbean as two separate areas because at least one species of Bembrops (B. magnisquamis) is endemic to the Caribbean. The southern part of the western Atlantic and the eastern Atlantic are also considered as separate areas. The Indo-West Pacific region is divided into five areas – Indian Ocean, Indo-Malayan area, southern Australia-New Zealand, Japan and Hawaii. New Zealand has only one representative – B. morelandi. B. nematopterus is endemic to the western Indian Ocean.

DISCUSSION

The past geological events of the earth are documented in various publications (Ekman, 1953; Briggs, 1974, 1987; Hallam, 1981; Kennett, 1982; Pough et al., 1989). Some of these events, which are of interest in connection with the origin and evolutionary history of Bembrops, are presented here. During most of the early Cenozoic, the marine fauna of the Atlantic and the western Pacific freely exchanged via the Tethys Sea. During the Eocene, Australia started to move north, away from Antarctica, creating major changes in oceanic climate and biogeography. The final closure of the Tethys Sea in the Mediterranean region occurred about 18 million years ago during the Miocene when Africa collided with Europe and sealed off the Tethyan Seaway. During the Pliocene (3-5 million years ago), the Panamanian Seaway closed by the final completion of the Isthmus of

Panama, blocking off any faunal exchange between the western Atlantic and the eastern Pacific. The Pleistocene is characterized by a number of glacial/interglacial events resulting in latitudinal temperature changes, sea level variations, fluctuations in oceanic circulation, etc. The sea level might have dropped considerably below normal resulting in a reduced bottom area and area on the outer shelf which, in turn, had considerable effect on the fauna of the continental shelf and slope. Based on these events, and considering the taxonomy and the distribution of the species of Bembrops, two explanations can be postulated for the origin of the genus.

Bembrops vandeveldae (Steurbaut, 1979) and B. smigielskae (Steurbaut, 1984) have been described from the otolith material from the Oligocene and Miocene of France indicating that the genus was possibly distributed in the Tethys Sea. This suggests a relatively long evolutionary history of the genus with its ancestral taxon having a broad Tethyan distribution from the Indo-Pacific through the Atlantic, and possibly including the eastern Pacific. Verification of the validity of the two fossil species and additional fossil material are needed to support this view.

Secondly, if the otolith fossil record is not valid, there are arguments suggesting that Bembrops arose relatively recently, in the last 3-5 million years. There are no records of any percophid from the American west coast, a fact that suggests that the members of this taxon could neither pass the eastern Pacific barrier, with its extensive stretches of deep water and few islands between Polynesia and the American continent, nor cross the Isthmus of Panama when it was submerged. The first barrier also proves to be a major obstacle for the successful dispersal of many shallow-water ostracods (Witte and van Harten, 1991) and continental shelf faunas in general (Ekman, 1953). For the latter barrier, the presence of four species of Bembrops in the Gulf of Mexico and the Caribbean Sea also suggests that the group must have appeared in this region after the final completion of the Isthmus of Panama about 3-5 million years ago, so that the continental land mass acted as a

barrier for further dispersal toward the American west coast. This, in turn, indicates that the genus evolved or reached the Atlantic sometime after the final closure of the Panamanian Seaway. In my view, this explanation seems to be more logical than a pre-Tethyan or Tethyan origin.

The geographic distributions of the node III species group suggest a historic connection between eastern South America and the Caribbean-Gulf of Mexico area. B. anatirostris and B. gobioides are restricted to the Caribbean and the Gulf of Mexico. B. heterurus shows an amphi-Atlantic distribution with its presence in the eastern Atlantic and only in the southern part of the western Atlantic along the coast of Brazil. B. caudimaculata forms a sister-group relationship with B. heterurus and is represented in the eastern Atlantic. A combination of vicariant events and dispersal was hypothesized to explain the distributions of the Atlantic gadoid family Merlucciidae (Ho, 1990). The hypothesis states that the ancestral group originated in the northern Atlantic and then dispersed into low-latitude continental shelve waters during the late Eocene, expanding its range further east, during lower sea level. The historical events of the hypothesis are supported by other Atlantic gadoids, as documented by Howes (1991). The distributional pattern of the node III species group of Bembrops has a similar pattern that could represent a dispersal or vicariant event.

Springer (1982) described the Pacific Plate as "a biogeographic region of major significance" based on his observation of the distributional patterns of numerous shorefish taxa. For the purpose of comparison, I have considered this area as a generalized track, which, along with the Indo-West Pacific track of Vari (1978), constitute the two major tracks within the Indo-Pacific. The distribution of most species of the node IV and V species groups strongly support the distributional patterns of the family Teraponidae, hence approximating the generalized Indo-West Pacific track of Vari (1978). Springer (1982) also demonstrated numerous distributional patterns among shorefishes that fit the Indo-West

Pacific track, the two tracks being separated at the western margin of the Pacific lithospheric plate. There is only one representative of Bembrops (B. filifera) that is present within the Pacific Plate area only in Hawaii, and it is well represented in the Indo-West Pacific area. If we assume that the apparent absence of B. filifera from the mid Pacific Plate region other than the Hawaiian Islands is not a collecting artifact, then at least one dispersal and/or regional extinction event must be responsible for the current distribution of the species. Starnes (1988) presented a similar scenario for the distribution of Priacanthus blochii species group. B. morelandi is endemic to New Zealand and is located just outside the margin of the Pacific Plate. The latter species is known only by the holotype and a paratype, and was only recently described. Future collections may expand its range within the Pacific Plate track.

The distributional patterns of the node IV species group comprise two subunits, Indo-West Pacific and Pacific Plate, and Caribbean and Gulf of Mexico. The geographic distribution of B. platyrhynchus encompasses the distribution of B. curvatura and B. filifera within the Indo-Malayan area and further extends into the western Indian Ocean. B. curvatura, B. platyrhynchus and B. filifera together are sister to B. macromma which is distributed in the Gulf of Mexico and the Caribbean Sea.

Within the node V species group there are also at least two subunits. B. caudimacula is the most widespread species and occurs from Japan, Indo-Malay, northern Australia, Indian Ocean, Red Sea and also from the eastern Atlantic. Two endemic species within the Indo-West Pacific and Pacific Plate area are its closest relatives, B. morelandi from New Zealand and B. nematopterus from the western Indian Ocean. These three species approximate the Indo-West Pacific track with an expanded element for B. caudimacula in the eastern Atlantic. B. magnisquamis is the sister-group to the above mentioned clade and occurs in the Caribbean Sea. The fifth species of this node, B. greyi,

is distributed along the coasts of Guinea, Gabon, Congo, and Angola in the eastern Atlantic. An amphi-Atlantic track is hypothesized for these two species.

The allopatric occurrence of B. macromma of the node IV species group and B. magnisquamis of the node V species group in the Gulf of Mexico and the Caribbean Sea can be envisaged from the point of view of the origin and the evolutionary history of the genus. If the early ancestors of the node IV and V had a broad Tethyan distribution, then extinction from the eastern Atlantic and the Indo-West Pacific must be assumed. A post-Tethyan origin, on the other hand, would suggest a east-ward dispersal of the ancestors of the Indo-Pacific members. The members of the node III species group show a predominant Atlantic-Gulf of Mexico-Caribbean distribution and possibly appeared earlier. Among the four percophid genera studied in this study, Percophis represents the most primitive lineage and is recorded only from the southwestern Atlantic. Therefore, a dispersal event from the Atlantic toward the Indo-West Pacific can be suggested.

Briggs (1987) considered the East Indies area of the Indo-Pacific to be the "center of evolutionary radiation for the marine biota of the Indo-West Pacific region and to some extent, for the rest of the tropical marine world." The distributional patterns of the species of Bembrops (Fig. 7.2) show that this area is inhabited by at least four species. The Caribbean-Gulf of Mexico area is also occupied by four species. The phylogenetic analysis suggests that two of the Caribbean-Gulf of Mexico species (B. macromma and B. magnisquamis) are phylogenetically closer to the Indo-West Pacific species, but a hypothesis of dispersal of these two species from the Indo-west Pacific cannot be argued as the reason for their present distribution. Therefore, based on the information available at present, we cannot consider the part of the Indo-West Pacific as the more plausible area of center of origin for Bembrops. Of course, a definitive decision can only be reached by comparing the distributional patterns and phylogenetic relationships of all included taxa of the family Percophidae.

Based on the analysis of the distribution of Bembrops from the points of view of the three major biogeographic methodologies, it can be inferred that none of the methods are able to provide evidence for a complete explanation for the present distribution of the taxon. Both dispersal and plate-tectonic events play a major role in the scenario of biogeography of any taxon (Briggs, 1987). Study of the distributional patterns of 13 species of Bembrops does support this view. The area cladogram (Fig. 7.2) predicts that the validity of the generalized tracks discussed in the 'track analysis' section will be congruent with area cladograms for other taxa with similar distributional patterns, but this can only be tested as phylogenetic analyses of additional taxa become available.

8. GENERAL DISCUSSION

This study has presented the taxonomy and phylogeny of the genus Bembrops based on the comparative morphology and osteology of all valid species of the genus. There have been two major goals in this context: 1) to provide a taxonomic revision of the species in the genus; 2) to establish the phylogenetic scheme for the species.

Bembrops can be identified as a phenotypically distinct taxon of the Percophidae based on the presence of a number of characteristic features, such as the flattened snout with the lower jaw protruding beyond the upper jaw, very narrow interorbital width, large eyes, six spines on the first dorsal fin, and the maxillary tentacle. It shares many of these features with its sister taxon Chrionema. Since 1876, 18 species have been described in this genus. A detailed examination of 26 morphometric characters, 21 truss characters, 14 meristic characters and two subjectively quantified attributes on some 720 specimens has revealed more intraspecific variation than has been reported in the earlier literature. Principal components analysis is a relatively less biased statistical procedure to study the extent of variation, and it was useful in distinguishing most of the valid species. The results of the analysis have led to the conclusion that a number of species are not actually distinct from each other. As a result, five species have been synonymized with other species. B. adenensis was synonymized with B. caudimacula. B. filodorsalia and B. indica were recognized as junior synonyms of B. filifera. B. aethalea and B. philippinus were inferred to be synonymous with B. platyrhynchus. The results also show that a number of meristic characters and attributes were more powerful than morphometric characters in discrimination. Where principal components analysis was not successful in discriminating all specimens of certain species groups (such as species clusters of B. caudimacula and B. platyrhynchus), additional characters (e. g., pigmentation on membranes between spines of the first dorsal fin) were used in making a decision in favor of the separate species

status. Very small samples were available for at least four species (B. caudimaculata, B. nematopterus, B. greyi and B. morelandi). Any additional material would be useful to reconfirm their species status.

The phylogenetic study was conducted with a data matrix of 54 morphological and osteological characters. An outgroup comparison method was employed in the analysis. Nelson (1984) recognized three lineages in the family Percophidae. Percophis brasiliensis, Chrionema chlorotaenia, C. squamiceps and Hemerocoetes pauciradiatus, representing all three lineages, were used as members of the outgroup. The hypothesis of phylogenetic relationships for the four percophid genera presented in Fig. 6.1 is well substantiated by a number of well-defined synapomorphies. In comparison, relationships at the species level (Fig. 6.11) are much less well-corroborated due to the presence of a number of homoplasies. With the available data, it was not possible to refine the hypothesis of species-level relationships. Starnes (1988) provided similar evidence in his study of the phylogeny of the priacanthids.

All 13 species of Bembrops share at least seven apomorphies to infer the monophyly of the genus. As is apparent from their overall morphological similarity, Bembrops has a sister-group relationship with Chrionema, supported by seven synapomorphies. Among the four genera used in this study, Percophis certainly represents the most primitive lineage within the family Percophidae with the presence of a number of plesiomorphic states, such as higher number of first dorsal fin spines and caudal fin rays, presence of predorsal bones, and presence of more vomerine teeth. Hemerocoetes proved to be the most apomorphic with the loss of spinous dorsal fin, palatine teeth, and pelvic processes, and fusion of the hypural bony elements.

Within the genus, three species groups are recognized: species of the primarily Atlantic B. anatirostris species group (node III species group) include B. anatirostris, B. gobioides, B. caudimaculata and B. heterurus; species of the mostly Indo-West Pacific B. curvatura species group (node IV species group) include B. curvatura,

B. platyrhynchus, B. filifera and B. macromma; and species of the Indo-West Pacific and Atlantic B. caudimacula species group (node V species group) include B. caudimacula, B. morelandi, B. nematopterus, B. magnisquamis and B. greyi.

The distributional patterns of the species of Bembrops raise questions regarding the mechanisms accounting for their present-day distribution. A comparative analysis of the three major biogeographic methods suggest a combination of dispersal and vicariance as driving forces for the current distributional patterns.

The hypothesis of interrelationships of the species of Bembrops presented in this thesis is provisional. It is not my intention to present the results of this study as the "final word" on this group of fishes. Further investigation is needed in other areas to test my hypothesis, including a detailed phylogenetic study of relationships among all members of the family Percophidae.

9. LITERATURE CITED

ALCOCK, A. 1893. Natural history notes from H. M. Indian Marine Survey Steamer 'Investigator', Comm. C. F. Oldham, R. N., Commanding. Series II., No. 9. An account of the deep sea collection made during the season 1892-93 [Vertebrata]. J. Asiat. Soc. Beng. 62: 177-184.

ALCOCK, A. 1894. Natural history notes from H. M. Indian Marine Survey Steamer 'Investigator', Comm. C. F. Oldham, R. N., Commanding. Series II., No. 11. An account of a recent collection of bathybial fishes from the Bay of Bengal and from the Laccadive Sea. J. Asiat. Soc. Beng. 63: 115-137.

ALCOCK, A. 1899. A Descriptive Catalogue of the Indian Deep-Sea Fishes in the Indian Museum. Indian Museum, Calcutta.

ALCOCK, A. 1902. A Naturalist in Indian Seas. John Murray, London. 328 pp.

ANDERBERG, A., and A. TEHLER. 1990. Consensus trees, a necessity in taxonomic practice. Cladistics 6: 399-402.

ATCHLEY, W. R., and D. ANDERSON. 1978. Ratios and statistical analysis of biological data. Syst. Zool. 27: 71-77.

ATCHLEY, W. R., C. T. GASKINS, and D. ANDERSON. 1976. Statistical properties of ratios. I. Empirical results. Syst. Zool. 25: 137-148.

BERG, L. S. 1940. Classification of fishes, both recent and fossil. Trav. De l'Inst. Zool. De l'Acad. Des Sci. De l'URSS 5: 87-517.

BOOKSTEIN, F. L., B. CHERNOFF, R. ELDER, J. HUMPHRIES, G. SMITH, and R. STRAUSS. 1985. Morphometrics in Evolutionary Biology. Acad. Nat. Sci. Philadel., Spl. Publ. 15, 277 pp.

BOULENGER, G. A. 1901. Notes on the classification of teleostean fishes.-I. On the Trachinidae and their allies. Ann. Mag. Nat. Hist. Ser. 7, 8: 261-271.

BRIGGS, J. C. 1974. Marine Zoogeography. McGraw-Hill Book Co., New York. 475 pp.

BRIGGS, J. C. 1984. Centres of Origin in Biogeography. Biogeographical Monograph 1. Biol. Study Group, University of Leeds, Leeds. 95 pp.

BRIGGS, J. C. 1987. Biogeography and Plate Tectonics. Elsevier, Amsterdam. 203 pp.

BROOKS, D. R. 1981. Hennig's parasitological method: a proposed solution. Syst. Zool. 30: 229-249.

BROOKS, D. R. 1988. Macroevolutionary comparisons of host and parasite phylogenies. Ann. Rev. Ecol. Syst. 19: 235-259.

BROOKS, D. R. 1990. Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. Syst. Zool. 39: 14-30.

CADENAT, J. 1937. Recherches systematiques sur les poissons littorauxde la cote occidentale d'Afrique. Revue des Travaux de l'Office des Peches Maritimes 10: 425-562.

CARPENTER, J. M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291-296.

CHANDLER, C. R., and M. H. GROMKO. 1989. On the relationship between species concepts and speciation processes. Syst. Zool. 38: 116-125.

CHARIG, A. J. 1982. Systematics in biology: a fundamental comparison of some major schools of thought. pp. 363-440. In: Problems of phylogenetic reconstruction. K. A. Joysey, and A. E. Friday (eds.). Academic Press, London and New York.

CRAW, R. 1982. Phylogenetics, areas, geology and the biogeography of Croizat: a radical view. Syst. Zool. 31: 304-316.

CROIZAT, L. 1982. Vicariance/vicariism, panbiogeography, "vicariance biogeography", etc.: a clarification. Syst. Zool. 31: 291-304.

DARLINGTON, P. J., Jr. 1957. Zoogeography: the Geographical Distribution of Animals. John Wiley, New York. 675 pp.

EKMAN, S. 1953. Zoogeography of the Sea. Sidgwick & Jackson Ltd., London. 417 pp.

ESCHMEYER, W. N. 1990. Catalog of the Genera of the Recent Fishes. Calif. Acad. Sci., San Francisco. 697 pp.

FOWLER, H. W. 1938. Descriptions of new fishes obtained by the United States Bureau of Fisheries steamer "Albatross", chiefly in Philippine seas and adjacent waters. Proc. U.S. Nat. Mus. 85: 31-135.

FOWLER, H. W. 1939. Ichthyological notes. No. 1. Not. Nat. Acad. Nat. Sci. Phila. 1939, No. 3: 1-2.

GILBERT, C. H. 1905. The deep-sea fishes of the Hawaiian Islands. Bull. U.S. Fish Comm. 23: 577-713.

GINSBURG, I. 1955. Fishes of the family Percophididae from the coasts of eastern United States and the West Indies, with descriptions of four new species. Proc. U.S. Nat. Mus. 104: 623-639.

GOODE, G. B. 1880. Descriptions of seven new species of fishes from deep soundings on the southern New England coast, with diagnoses of two undescribed genera of flounders and a genus related to Merlucius. Proc. U.S. Nat. Mus. 3: 337-350.

GOODE, G. B., and T. H. BEAN. 1896. Oceanic Ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers Blake, Albatross, and Fish Hawk in the northwestern Atlantic, with an atlas containing 417 figures. Spec. Bull. U.S. Nat. Mus. No. 2: Text: xxxv + 26 + 553 pp., Atlas: xxiii + 26 + 123 pls.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, and G. S. MYERS. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. Bull. Amer. Nat. Hist. 131 (art. 44). 455 pp.

GREY, M. 1959. Deep sea fishes from the Gulf of Mexico with the description of a new species Squalogadus intermedius (Macrouroididae). Fieldiana, Zool. 39: 323-346.

HALLAM, A. 1981. Relative importance of plate movements, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic. pp. 303-330. In: G. Nelson, and D. E. Rosen (eds.). Vicariance Biogeography: a critique. Columbia Univ. Press, New York. 593 pp.

HENDY, M. D., and D. PENNY. 1982. Branch and bound algorithms to determine minimal evolutionary trees. Math. Biosc. 59: 277-290.

HO, J. -S. 1990. Phylogeny and biogeography of hakes (Merluccius; Teleostei) a cladistic analysis. U.S. Fish. Bull. 88: 95-104.

HOWES, G. J. 1991. Biogeography of gadoid fishes. J. Biogeogr. 18: 595-622.

HUBBS, C. L., and K. F. LAGLER. 1964. Fishes of the Great Lakes region. University of Michigan Press, Ann Arbor, Michigan. 213 pp.

HUMPHRIES, C. J., and L. R. PARENTI. 1986. Cladistic Biogeography. Oxford Monographs on Biogeography No. 2. Claredon Press, Oxford. 98 pp.

HUMPHRIES, J. M., F. L. BOOKSTEIN, B. CHERNOFF, G. R. SMITH, R. L. ELDER, and S. G. POSS. 1981. Multivariate discrimination by shape in relation to size. Syst. Zool. 30: 291-308.

IWAMOTO, T., and J. C. STAIGER. 1976. Percophidid fishes of the genus Chrionema Gilbert. Bull. Mar. Sci. 26: 488-498.

JORDAN, D. S. 1923. A classification of fishes including families and genera as far as known. Stanford Univ. Publ. Univ. Ser., Biol. Sci. 3: 77-243.

JORDAN, D. S., and B. W. EVERMANN. 1896. The fishes of North and Middle America. Bull. U.S. Nat. Mus. No. 47. 3313 pp.

JORDAN, D. S., and J. O. SNYDER. 1902. A review of the trachinoid fishes and their supposed allies found in the waters of Japan. Proc. U.S. Nat. Mus. 24: 461-497.

JORDAN, D. S., and A. SEALE. 1906. The fishes of Samoa. Description of the species found in the archipelago, with a provisional check-list of the fishes of Oceania. Bull. Bur. Fish. 25: 173-488.

KENNETT, J. P. 1982. Marine Geology. Prentice-Hall, Inc., New York. 813 pp.

KNAPP, L. W. 1981. Family Percophidae. pp. 1-6. In: FAO species identification sheets for fishery purposes. Eastern Central Atlantic; Fishing Areas 34, 47 (in part). W. Fischer, G. Bianchi, and W. B. Scott (eds.). Canada Funds-in-Trust, Dept. Fisheries and Oceans Canada, Ottawa, by arrangement with the Food and Agriculture Organization of the United Nations.

KURODA, N. 1950. A research on Bembrops caudimacula Steindachner. Jap. J. Ichthyol. 1: 57-61.

LEVITON, A. E., R. H. GIBBS, Jr., E. HEAL, and C. E. DAWSON. 1985. Standards in Herpetology and Ichthyology: Part I. Standard symbolic codes for Institutional resource collections in Herpetology and Ichthyology. Copeia 1985: 802-832.

LINDBERG, G. U., and Z. V. KRASYUKOVA. 1969. Fishes of the Sea of Japan and the Adjacent Areas of the Sea of Okhotsk and the Yellow Sea. Part 3. Izdatel'stvo "Nauka", Leningrad (in Russian). Eng. trans. Israel Progr. Sci. Publ., Jerusalem. 1977. 498 pp.

MADDISON, W. P., M. J. DONOGHUE, and D. R. MADDISON. 1984. Outgroup analysis and parsimony. Syst. Zool. 33: 83-103.

MADDISON, W. P., and D. R. MADDISON. 1988. MacClade. An interactive, graphic program for analyzing phylogenies and studying character evolution. Version 2.96c. Harvard University, Cambridge.

MAYDEN, R. L. 1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. Syst. Zool. 37: 329-355.

MAYR, E., and P. D. ASHLOCK. 1991. Principles of Systematic Zoology. McGraw-Hill, Inc., New York. 475 pp.

MCKAY, R. J. 1971. Two new genera and five new species of percophidid fishes (Pisces: Percophididae) from Western Australia. J. Roy. Soc. West. Austr. 54: 40-46.

MICKEVICH, M. F., and J. S. FARRIS. 1981. The implications of congruence in Menidia. Syst. Zool. 30: 351-370.

MILLER, G. L., and S. C. JORGENSEN. 1973. Meristic characters of some marine fishes in the western Atlantic ocean. Fish. Bull. 71: 301-312.

MIYAMOTO, M. M. 1985. Consensus cladograms and general classification. Cladistics 1: 186-189.

NELSON, G. 1985. A decade of challenge the future of biogeography. pp. 187-196. In: Plate Tectonics and Biogeography. A. E. Leviton, and M. L. Aldrich (eds.). Earth Sciences History (J. Hist. Earth Sci. Soc.), vol. 4.

NELSON, G., and N. PLATNICK. 1981. Systematics and Biogeography: Cladistics and Vicariance. Columbia University Press, New York. 567 pp.

NELSON, J. S. 1978. Bembrops morelandi, a new percophidid fish from New Zealand, with notes on other members of the genus. Rec. Nat. Mus. N.Z. 1: 237-241.

NELSON, J. S. 1979. Revision of the fishes of the New Zealand genus Hemerocoetes (Perciformes: Percophididae), with descriptions of two new species. N.Z. J. Zool. 6: 587-599.

NELSON, J. S. 1982. Pteropsaron heemstrai and Osopsaron natalensis (Perciformes: Percophidae), new fish species from South Africa, with comments on Squamicreedia obtusa from Australia and on the classification of the subfamily Hemerocoetinae. J. L. B. Smith Instt. Ichthyol. Spl. Publ. No. 25, 11 pp.

NELSON, J. S. 1984. Fishes of the World. 2nd ed. John Wiley & Sons, New York. 523 pp.

NELSON, J. S. 1986. Some characters of Trichonotidae, with emphasis to those distinguishing it from Creediidae (Perciformes: Trachinoidei). Jap. J. Ichthyol. 33: 1-6.

NORMAN, J. R. 1939. Fishes. Scientific Reports of the John Murray Expedition 1933-34. Zoology 7: 1-116.

OKADA, Y., and K. SUZUKI. 1952. On two new bembroid fishes from the deep sea off Mie Prefecture with special reference in relation to hitherto known species. Rep. Fac. Fish., Prefec. Univ. Mie 1: 67-74.

OKAMURA, O., K. AMAOKA, and F. MITANI. 1982. Fishes of the Kyushu-Palau Ridge and Tosa Bay. The intensive research of unexploited fishery resources on continental slopes. Jap. Fish. Resource Conserv. Assn., Tokyo, Japan. 435 pp.

OKAMURA, O., and S. KISHIDA. 1963. A new genus and species of the bembroid fish collected from the Bungo Channel, Japan. Bull. Misaki Mar. Biol. Inst. 4: 43-48.

PIETSCH, T. W. 1989. Phylogenetic relationships of trachinoid fishes of the family Uranoscopidae. Copeia 1989: 253-303.

PIETSCH, T. W., and C. P. ZABETIAN. 1990. Osteology and interrelationships of the sand lances (Teleostei: Ammodytidae). Copeia 1990: 78-100.

PLATNICK, N., and G. J. NELSON. A method of analysis for historical biogeography. Syst. Zool. 27: 1-16.

POLL, M. 1959. Poissons. V. Teleosteens Acanthopterygiens. Res. Sci. Exped. Ocenogr. Belge Cot. Afr. l'Atlant. Sud (1948-1949) 4: 1-417.

POUGH, F. H., J. B. HEISER, and W. N. MCFARLAND. 1989. Vertebrate Life. 3rd ed. Macmillan Publ. Co., New York. 904 pp.

QUOY, J. R. C., and J. P. GAIMARD. 1824-25. Description des Poissons. Chapter IX. (In: Freycinet, L. de. Voyage autour du Monde...exécuté sur les corvettes de L. M. "L'Uranie" et "La Physicienne," pendant les années 1817, 1818, 1819 et 1820. Paris.). pp. 192-401 [1-328 in 1824; 329-616 in 1825], Atlas pls. 43-65.

REGAN, C. T. 1913. The classification of the percoid fishes. Ann. Mag. Nat. Hist. 12: 111-145.

RIBEIRO, A. M. 1915. Peixes. V. Physoclisti. In: Fauna Brasiliense. Arch. Mus. Nac. Rio de Janeiro. 17.

RICHARDS, W. J. 1990. List of the fishes of the western central Atlantic and the status of early life stage information. NOAA Tech. Mem. NMFS-SEFC-267. 87 pp.

ROJO, A. L. 1991. Dictionary of Evolutionary Fish Osteology. CRC Press, Boca Raton. 273 pp.

ROSEN, D. E. 1976. A vicariance model of Caribbean biogeography. Syst. Zool. 24: 431-464.

ROSEN, D. E. 1978. Vicariant patterns and historical explanation of biogeography. Syst. Zool. 27: 159-188.

SCHULTZ, L. P. 1960. Family Mugiloididae and family Trichonotidae. In: L. P. Schultz et al. Fishes of the Marshall and Marianas Islands. Vol. 2. Bull. U.S. Nat. Mus. 202: 266-281.

SMITH, J. L. B. 1965. The Sea Fishes of Southern Africa. Central News Agency Ltd., South Africa. 580 pp.

SPRINGER, V. G. 1982. Pacific Plate biogeography, with special reference to shorefishes. Smiths. Contr. Zool. No. 367L 1-182.

STAIGER, J. C. 1970. The distribution of the benthic fishes found below two hundred meters in the Straits of Florida. PhD Thesis, University of Miami, Coral Gables. 219 pp.

STARNES, W. C. 1988. Revision, phylogeny and biogeographic comments on the circumtropical marine percoid fish family Priacanthidae. Bull. Mar. Sci. 43: 117-203.

STEINDACHNER, F. 1876. Ichthyologische Beitrage. V. Sitzung. Akad. Wiss. Wien 74: 49-240.

STEURBAUT, E. 1979. Les otolithes de Téléostéens des Marnes de Saubrigues (Miocene d'Aquitaine meridionale, France). Palaeontographica Abt. A, 166: 48-91.

STEURBAUT, E. 1984. Les otolithes de Téléostéens de l'Oligo-Miocene d'Aquitaine (Sud-Ouest de la France). Palaeontographica Abt. A, 186: 1-162.

STEVENS, P. F. 1980. Evolutionary polarity of character states. Ann. Rev. Ecol. Syst. 11: 333-358.

STEYSKAL, G. C. 1980. The grammar of family-group names as exemplified by those of fishes. Proc. Biol. Soc. Wash. 93: 168-177.

STRAUSS, R. E., and F. L. BOOKSTEIN. 1982. The truss: body form reconstructions in morphometrics. Syst. Zool. 31: 113-135.

SWOFFORD, D. L. 1991. PAUP: Phylogenetic Analysis using Parsimony. Version 3.0s. Illinois Natural History Survey, Champaign. 178 pp.

TAKI, I. 1953. On two new species of fishes from the Inland Sea of Japan. J. Sci. Hiroshima Univ., B. Div. 1, 14: 201-210.

TAYLOR, W. R., and G. C. VAN DYKE. 1985. Revised procedures for staining and clearing fishes and other vertebrates for bone and cartilage study. Cybium 9: 107-119.

TINKER, S. W. 1978. Fishes of Hawaii. A Handbook of the Marine Fishes of Hawaii and the Central Pacific Ocean. Hawaiian Service Inc., Honolulu. 532 pp.

VARI, R. P. 1978. The terapon perches (Percoidei, Teraponidae): a cladistic analysis and taxonomic revision. Bull. Am. Mus. Nat. Hist. 159: 175-340.

WATROUS, L. E., and Q. D. WHEELER. 1981. The out-group comparison method of character analysis. Syst. Zool. 30(1): 1-11.

WILEY, E. O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. Wiley-Interscience, New York. 439 pp.

WILEY, E. O., D. SIEGEL-CAUSEY, D. R. BROOKS, and V. A. FUNK. 1991. The Compleat Cladist: A Primer of Phylogenetic Procedures. Spl. Publ., Univ. Kansas, No. 19, 158 pp.

WITTE, L., and VAN HARTEN, D. 1991. Polymorphism and systematics of Kotoracythere inconspicua (Brady, 1880) (Ostracoda: Pectocytheridae).

ZEHREN, S. J. 1987. Osteology and evolutionary relationships of the boarfish genus Antigonia (Teleostei: Caproidae). Copeia 1987: 564-592.

APPENDIX I

MORPHOMETRIC CHARACTERS

1. Total length (TL).
2. Standard length (SL).
3. Head length (HDL).
4. Head width (HDW).
5. Head height (HDH).
6. Length of orbit (EYD).
7. Snout length (SNL).
8. Postorbital length (POL).
9. Length of maxillary tentacle (TNTL).
10. Length of upper jaw (UPJL).
11. Body depth (BDD).
12. Predorsal length (1^{st}) (PRDR1).
13. Predorsal length (2^{nd}) (PRDR2).
14. Postdorsal length (1^{st}) (PSDR1).
15. Postdorsal length (2^{nd}) (PSDR2).
16. Length of pectoral fin (PECFL).
17. Interpectoral distance (INPECD).
18. Length of pelvic fin (PELFL).
19. Interpelvic distance (INPELD).
20. Interorbital width (IOW).
21. Length of caudal peduncle (LCPD).
22. Depth of caudal peduncle (HCPD).

23. Length of 1st dorsal fin base (DRFNB1).
24. Length of 2nd dorsal fin base (DRFNB2).
25. Length of anal fin base (ANLFNB).
26. Anus to origin of anal fin (ANSANL).

MERISTIC CHARACTERS

1. Lateral line scales (LATL).
2. Scales above lateral line (LATTR).
3. 1st dorsal fin spines (DRF1S).
4. 2nd dorsal fin rays (DRF2R).
5. Pectoral fin rays (PECFR).
6. Pelvic fin spine (PELFS).
7. Pelvic fin rays (PELFR).
8. Anal fin rays (ANLFR).
9. Caudal fin rays (CAUDFR).
10. Gill rakers on upper limb (GLRUL).
11. Gill rakers on lower limb (GLRLL).
12. Branchiostegal rays (BRACSTGL).
13. Rows of scales between 1st ray of anal fin and lateral line (ANLLTSF).
14. Rows of scales between last ray of anal fin and lateral line (ANLLTSL).

ATTRIBUTES

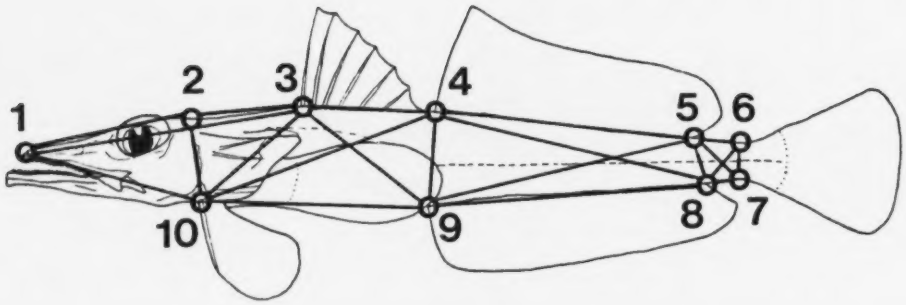
1. Slope of lateral line (LATLSLP).
2. Color of peritoneum (PRTNM).

APPENDIX II

TRUSS CHARACTERS (= Interlandmark distances) (Fig. II.1)

1. TRUSS 1: Tip of upper jaw to end of occiput (1-2).
2. TRUSS 2: Tip of upper jaw to origin of 1st dorsal fin (1-3).
3. TRUSS 3: End of parietal to origin of 1st dorsal fin (2-3).
4. TRUSS 4: Origin of 1st dorsal fin to origin of 2nd dorsal fin (3-4).
5. TRUSS 5: Origin of 2nd dorsal fin to posterior base of 2nd dorsal fin (4-5).
6. TRUSS 6: Posterior base of 2nd dorsal fin to dorsal fin hypural plate (5-6).
7. TRUSS 7: Dorsal hypural plate to ventral hypural plate (6-7).
8. TRUSS 8: Ventral hypural plate to posterior base of anal fin (7-8).
9. TRUSS 9: Posterior base of anal fin to origin of anal fin (8-9).
10. TRUSS 10: Origin of anal fin to origin of pelvic fin (9-10).
11. TRUSS 11: Tip of upper jaw to origin of pelvic fin (1-10).
12. TRUSS 12: End of parietal to origin of pelvic fin (2-10).
13. TRUSS 13: Origin of 1st dorsal fin to origin of pelvic fin (3-10).
14. TRUSS 14: Origin of 2nd dorsal fin to origin of pelvic fin (4-10).
15. TRUSS 15: Origin of 1st dorsal fin to origin of anal fin (3-9).
16. TRUSS 16: Origin of 2nd dorsal fin to origin of anal fin (4-9).
17. TRUSS 17: Posterior base of 2nd dorsal fin to origin of anal fin (5-9).
18. TRUSS 18: Origin of 2nd dorsal fin to posterior base of anal fin (4-8).
19. TRUSS 19: Posterior base of 2nd dorsal fin to posterior base of anal fin (5-8).
20. TRUSS 20: Dorsal hypural plate to posterior base of anal fin (6-8).
21. TRUSS 21: Posterior base of 2nd dorsal fin to ventral hypural plate (5-7).

Fig. II.1. Truss network for species of Bembrops. Locations of 10 landmarks are illustrated as open circles and morphometric distance measures between circles as solid lines. See Appendix II for details.


1
2
3
4
5
6
7
8
9
10

APPENDIX III

The following abbreviations are used throughout the text and in illustrations for identification of osteological structures.

ANGL	Angular
ANPV	Anterior process of pelvic girdle
ARPM	Articulating process of premaxilla
ASPM	Ascending process of premaxilla
BRST	Branchiostegal rays
BSHY	Basihyal
BSOC	Basioccipital
CLEI	Cleithrum
CORC	Coracoid
CRBR1-5	Ceratobranchials 1-5
CRHY	Ceratohyal
DENT	Dentary
DHYP	Dorsal hypohyal
DPCR	Dorsal procurrent rays
ECPT	Ectopterygoid
EPBR1-4	Epibranchials 1-4
EPHY	Epihyal
EPOT	Epiotic
EPUR1-3	Epurals 1-3
EXOC	Exoccipital
EXSC	Extrascapular

FRMG	Foramen Magnum
FRNT	Frontal
GLRK	Gillraker
HPUR1-5	Hypurals 1-5
HYBR1-3	Hypobranchials 1-3
HYOM	Hyomandibular
HYPP	Hypurapophysis
INCL	Intercalar
INFR2-4	Infraorbitals 2-4
INHY	Interhyal
INOP	Interopercle
LACR	Lacrymal
LETH	Lateral ethmoid
MAXL	Maxilla
MSET	Mesethmoid
MSPT	Mesopterygoid
MTPT	Metapterygoid
NASL	Nasal
OPER	Opercle
PALA	Palatine
PARI	Parietal
PCFR	Pectoral fin ray
PHBR1-4	Pharyngobranchials 1-4
PLFR	Pelvic fin ray
PLFS	Pelvic fin spine
PLSP	Pelvic spur

PMXL	Premaxilla
PRHP	Parhypural
PROP	Preopercle
PROT	Prootic
PSPH	Parasphenoid
PSPM	Postmaxillary process of premaxilla
PSPV	Posterior process of pelvic girdle
PTRT	Pterotic
PTTM	Posttemporal
QUAD	Quadrate
RART	Retroarticular
SBOP	Subopercle
SCAP	Scapula
SPHN	Sphenotic
SUCL	Supracleithrum
SUOC	Supraoccipital
SYMP	Symplectic
URHY	Urohyal
URNU	Uroneural
VHYP	Ventral hypohyal
VPCR	Ventral procurrent rays
VOMR	Vomer

APPENDIX IV

List of 54 characters used in the data matrix for the phylogenetic analysis of the genus Bembrops. The plesiomorphic state (State 0) is followed by apomorphic state(s) (State 1 or 2).

1. Lateral crest or spur on hyomandibular. State 0: absent; state 1: present.
2. Pelvic spur. State 0: absent; state 1: present.
3. Mesopterygoid. State 0: not forming the floor of the eye; state 1: forming the floor of the eye.
4. Anterior head of vomer. State 0: covered with small teeth on all its ventral surface; state 1: teeth restricted on ventrolateral edge.
5. Hyomandibular spur or crest. State 0: spur; state 1: crest (a further derived state of character 1).
6. Adult size. State 0: maximum total length greater than 400 mm; state 1: maximum total length not reaching beyond 350 mm.
7. Skeleton. State 0: heavier with sculpturing; state 1: lighter without sculpturing.
8. Predorsal bone. State 0: present; state 1: absent.
9. Teeth in premaxillary symphysis area. State 0: well developed, larger; state 1: relatively smaller in size.
10. Principal caudal fin rays. State 0: 13; state 1: 10 or 11.
11. Exposed spine on anterior tip of maxilla. State 0: absent; state 1: present.
12. Ascending process of premaxilla. State 0: shorter in length; state 1: longer.
13. Spinous dorsal fin. State 0: present; state 1: absent.
14. Teeth on palatine. State 0: present; state 1: absent.
15. Epurals. State 0: somewhat tubular; state 1: flat.

16. Hypurals. State 0: not fused; state 1: fused to form a dorsal and a ventral hypural plate.
17. Anterior and posterior processes on pelvic bone. State 0: present; state 1: absent.
18. Scapula and coracoid. State 0: extended to reach posterolateral margin of cleithrum; state 1: not extended.
19. Nasal bone. State 0: not goblet shaped; state 1: goblet shaped.
20. Sixth branchiostegal ray. State 0: on epihyal; state 1: on ceratohyal or on cerato-epihyal junction.
21. Scales. State 0: mostly cycloid; state 1: ctenoid.
22. Number of opercular spine. State 0: 1; state 1: 2.
23. Preopercular spine. State 0: absent; state 1: present.
24. Urohyal. State 0: simple; state 1: complex.
25. Lacrymal and second infraorbital. State 0: connected to each other; state 1: a distinct gap between two bones.
26. Number of vertebrae. State 0: more than 28; state 1: 27 or 28.
27. Number of dorsal procurrent rays. State 0: 2; state 1: 7-11; state 2: 13-15.
28. Number of ventral procurrent rays. State 0: 1; state 1: 5-9; state 2: 11-13.
29. Maxillary tentacle. State 0: absent; state 1: present.
30. Indentation on posterior tip of maxilla. State 0: shallow; state 1: deep.
31. Medial bony plate-like connection of palatine. State 0: present; state 1: absent.
32. Proximal end of third branchiostegal ray. State 0: narrower; state 1: wider.
33. Number of spines on spinous dorsal fin. State 0: 9; state 1: 6.
34. Pterygiophores between spinous and soft dorsal fin. State 0: present; state 1: absent.
35. Scales on cheek. State 0: present; state 1: absent.
36. Number of gill rakers on lower limb of gill arch. State 0: more than or equal to 15; state 1: less than 15.
37. Number of lateral line scales. State 0: more than 60; state 1: less than 60.

38. Color of peritoneum. State 0: lighter; state 1: darker.
39. First spine of spinous dorsal fin. State 0: not elongated; state 1: elongated.
40. Slope of lateral line. State 0: no slope; state 1: gradual slope; state 2: abruptly sloping.
41. Snout length. State 0: shorter (less than 3 times head length); state 1: longer (more than 3 times head length).
42. Shape of first epural. State 0: proximal end blunt; state 1: proximal end pointed.
43. Attachment between first and second hypural. State 0: unattached; state 1: partially or completely attached.
44. Spinous extension at posterodorsal tip of interopercle. State 0: absent; state 1: present.
45. Posterior process of pelvic bone. State 0: long; state 1: short.
46. Anterior process of pelvic bone. State 0: short; state 1: long.
47. Length of symplectic. State 0: shorter, not reaching upper margin of posterior notch of metapterygoid; state 1: longer, reaching upper margin of posterior notch of metapterygoid.
48. Dorsal margin of metapterygoid. State 0: flat; state 1: somewhat pointed.
49. Small fossa at posterolateral margin of hyomandibular. State 0: present; state 1: absent.
50. Basihyal. State 0: narrow and elongated anteriorly; state 1: wider, shorter anteriorly.
51. Third hypobranchial. State 0: extended anteriorly; state 1: not extended anteriorly.
52. Teeth on palatine. State 0: more rows anteriorly; state 1: less rows anteriorly (a further derived state of character 14).
53. Posteromedial edge of urohyal. State 0: not extended posteriorly; state 1: extended posteriorly.
54. Posterodorsal end of epihyal. State 0: notched; state 1: not notched.

APPENDIX V

LIST OF INSTITUTIONAL ABBREVIATIONS (following Leviton et al., 1985)

AMS	Australian Museum, Sydney South, New South Wales, Australia.
BMNH	British Museum (Natural History), London, England.
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA.
BSKU	Kochi University, Kochi, Japan.
CSIRO	Commonwealth Science & Industrial Research Organization, Hobart, Tasmania, Australia.
FRLM	Mie University, Mie, Japan.
FURG	Fundacao Universidade do Rio Grande, Rio Grande do sul, Brazil.
GCRL	Gulf Coast Research Laboratory Museum, Ocean Springs, Mississippi, USA.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
ISH	Universitat Hamburg, Hamburg, Germany.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MZUSP	Museu de Zoologica, Universidade de Sao Paulo, Sao Paulo, Brazil.
NHRM	Swedish Museum of Natural History, Stockholm, Sweden.
NMNZ	National Museum of New Zealand, Wellington, New Zealand.
NMV	Museum of Victoria, Melbourne, Victoria, Australia.
NMW	Naturhistorisches Museum Wien, Wien, Austria.
NSMT	National Science Museum, Tokyo, Japan.
NTM	Northern Territory Museum of Arts & Sciences, Darwin, Northern Territory, Australia.

QM	Queensland Museum, Brisbane, Queensland, Australia.
SIO	Scripps Institution of Oceanography, La Jolla, California, USA.
SMF	Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt, Germany.
UAMZ	University of Alberta Museum of Zoology, Edmonton, Alberta, Canada.
UF	University of Florida, Florida State Museum, Gainesville, Florida, USA.
USNM	National Museum of Natural History, Washington, D. C., USA.
VUW	Victoria University, Wellington, New Zealand.
WAM	Western Australian Museum, Perth, Western Australia, Australia.
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark.
ZSI	Zoological Survey of India, Calcutta, West Bengal, India.